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Structure and functioning of the eastern Scotian Shelf ecosystem before and after the collapse of groundfish stocks in the early 1990s[1]

Alida Bundy

Abstract: The fishery-induced collapse of the Atlantic cod (*Gadus morhua*) stock on the eastern Scotian Shelf has altered the species composition of this ecosystem. Ecopath mass-balance models of the ecosystem before and after the collapse were developed to explore how the structure, function, and key species of the ecosystem had changed. For the first time, an analysis of uncertainty was conducted to examine the effects of the uncertainty on model estimates. A comparison of the two Ecopath models indicated that although total productivity and total biomass of the ecosystem remained similar, there were changes in predator structure, trophic structure, and energy flow, many of which were robust to uncertainty. Biomass has significantly increased at trophic levels 3 and 4, and the composition of these trophic levels has changed as a result of the mean increase in trophic level of many species-groups. Piscivory has increased, presumably because of the high abundance of small pelagic fish, and the ratio of pelagic feeders to demersal feeders has increased from 0.3 to 3.0. Thus, the ecosystem has changed from a demersal-feeder-dominated system to a pelagic-feeder-dominated system. Although uncertainty remains concerning some model estimates, the ecosystem has been profoundly altered and exhibits classic symptoms of "fishing down the food web". However, overall system properties were generally conserved.

Résumé : L'effondrement du stock de morues franches (*Gadus morhua*) de la plate-forme néo-écossaise orientale causé par la pêche commerciale a changé la composition spécifique de cet écosystème. La mise au point de modèles de bilans massiques Ecopath avant et après l'effondrement permet d'explorer les changements de structure, de fonction et de dominance des espèces de l'écosystème. Pour la première fois, une analyse d'incertitude examine les effets de l'incertitude sur les estimations des modèles. Une comparaison des deux modèles Ecopath indique que, même si la productivité et la biomasse totales de l'écosystèmes sont demeurées semblables, il y a eu des changements dans la structure des prédateurs, le réseau trophique et le flux d'énergie, dont plusieurs sont robustes face à l'incertitude. La biomasse s'est accrue significativement aux niveaux trophiques 3 et 4 et la composition de ces niveaux trophiques s'est modifiée par une augmentation moyenne de niveau trophique chez plusieurs groupes d'espèces. L'ichtyophagie a augmenté à cause sans doute de la forte abondance de petits poissons pélagiques et le rapport pélagique : démersal a crû de 0,3 à 3,0. L'écosystème a donc changé d'un système à dominance démersale à un système à dominance pélagique. Bien qu'il reste une incertitude au sujet de certaines estimations, l'écosystème a subi une modification profonde et montre des symptômes classiques d'un système où l'on pêche de plus en plus bas dans le réseau trophique. Néanmoins, les propriétés générales du système se sont généralement maintenues.

[Traduit par la Rédaction]

Introduction

We hear about the global overexploitation of fisheries (e.g., Christensen et al. 2003; Myers and Worm 2003; Pauly and MacLean 2003), the collapse of fish stocks (e.g., Hutchings and Myers 1995; Baum et al. 2003), and changed ecosystems (Pauly et al. 1998). The marine ecosystems of eastern Canada are no exception to this common picture. In the early 1990s, Atlantic cod (*Gadus morhua*; hereinafter cod) and groundfish stocks collapsed or were severely depleted in the Newfoundland–Labrador Shelf, the Gulf of St. Lawrence, and the eastern Scotian Shelf. Total estimated biomass of cod was around 2 million tonnes (t) in the mid-1980s and fell to a little over 200 000 t in the early 1990s. On the Newfoundland–Labrador Shelf and eastern Scotian Shelf, this decrease exceeds 90%. These changes have had

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A. Bundy. Fisheries and Oceans Canada, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, NS B2Y 4A2, Canada (e-mail: bundya@mar.dfo-mpo.gc.ca).

[1]This paper is part of a series derived from the 2003 American Fisheries Society special symposium "Structure and Function of Continental Shelf Ecosystems: Then and Now", held in Québec City, Quebec (August 2003), and from the Department of Fisheries and Oceans (DFO) Strategic Science Fund project "Comparative Dynamics of Exploited Ecosystems in the Northwest Atlantic (CDEENA)".

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profound effects on the fishery and the livelihood of harvesters (Cashin 1993; Ommer 1995), but the impact on the ecosystem as a whole is less clear. The aim of this paper is to explore the impact of fishery-induced changes on the ecosystem of the eastern Scotian Shelf (Fig. 1).

Traditionally, the eastern Scotian Shelf ecosystem was composed of large stocks of gadoids such as cod and haddock (*Melanogrammus aeglefinus*), marine mammals, including grey seals (*Halichoerus grypus*), but few pelagic fish. Like the other east-coast ecosystems, the eastern Scotian Shelf has been fished for several hundreds of years (Zwanenburg 2003). Anecdotal information suggested that in the 1800s, large shoals of haddock were observed on Banquereau Bank, whereas only low numbers of haddock have been caught there during the DFO Research Vessel (RV) survey, which began in 1970. Therefore, even before the Scotian Shelf was systematically monitored by means of a multispecies trawl survey, anthropogenic changes had impacted the ecosystem. More recently, however, the collapse and closure of the groundfish fishery, the continued increase in grey seal abundance, and an increase in invertebrates and forage fishes on the eastern Scotian Shelf have led to renewed interest in the effects of fishing on the ecosystem. Reviews of the eastern Scotian Shelf ecosystem are given in Zwanenburg et al. (2002), Zwanenburg (2003), and Department of Fisheries and Oceans (2003*a*).

Concurrent with the changes in species abundance over the last 15 years, environmental conditions have changed on the eastern Scotian Shelf (Zwanenburg et al. 2002; Department of Fisheries and Oceans 2003*b*). There was a marked decrease in bottom temperature on the more easterly part of the eastern Scotian Shelf (Misaine Bank): the 5-year mean temperature at 100 m dropped significantly below the long-term mean (1971–2000) in the mid-1980s, falling to a low in the early 1990s. By the late 1990s, the temperature rose above normal. These temperature changes demarcate a 15-year period of cold water that is unusual for its intensity and duration. Cold water was also noted along the inshore regions of the eastern Scotian Shelf (Department of Fisheries and Oceans 2003*b*). Meanwhile on the western portion of the eastern Scotian Shelf (Emerald Basin), the bottom temperature at 250 m has been above average since the 1980s, owing to warm offshore slope waters penetrating the Shelf. These environmental changes are likely to affect the productivity of marine species inhabiting the area. For example, haddock (Frank et al. 2001; Mohn and Simon 2002) and cod (Fanning et al. 2003) on the eastern Scotian Shelf exhibited reduced growth and size at maturity and many other fish species had reductions in weight at length (Department of Fisheries and Oceans 2003*a*).

There are many ways to model an ecosystem. Mills and Fournier (1979) first modelled the Scotian Shelf using a simple food-web approach, with minimal data. They split the area into shelf (0–180 m) and slope (180–703 m) and concluded that there were basic differences between the systems, but that neither had sufficient primary production to support both the pelagic and benthic pathways. Based on a comparison with the North Sea, they also concluded that fish production in different areas could not be estimated simply on the basis of differences in primary production: the structure of ecosystems must also be taken into account. Building on the work of Mills and Fournier (1979), Mills (1980) concluded that compared with other northwest Atlantic ecosystems, less energy was available on the Scotian Shelf, although fish production was comparable.

Sinclair et al. (1984) updated the analyses by Mills and Fournier (1979) and Mills (1980) using RV-survey estimates of biomass and production for cod and haddock. They concluded that the differences previously estimated between the Scotian Shelf and slope areas and between the Scotian Shelf and the North Sea were not justified, based on the data used and the assumptions made, and that those conclusions were premature. Sinclair et al. (1984) suggested that there were more trophodynamic similarities than differences between these areas.

No attempt has been made to model the Scotian Shelf ecosystem for the last 20 years. Over this time period, more data have been collected, sampling techniques have become more sophisticated, and other tools have been developed to explore ecosystem structure and functioning. One such tool is Ecopath with Ecosim (Christensen et al. 2000), a mass-balance trophic model that has been widely used, including modelling of the Newfoundland–Labrador Shelf ecosystem (Bundy et al. 2000; Bundy 2001; Pitcher et al. 2002). Ecopath with Ecosim has been used to successfully reproduce ecosystem states, including the Baltic Sea (Harvey et al. 2003), Newfoundland–Labrador Shelf (Bundy 2001), and the Gulf of Thailand (Christensen 1998).

Ecopath with Ecosim is used here to explore the effects of fishing on the eastern Scotian Shelf ecosystem. Two time periods are modelled: the early 1980s, before the collapse of cod and other groundfish stocks, and the late 1990s, after the collapse. Model indices are compared between the two time periods to determine how the ecosystem may have changed, and whether its structure and functioning have been affected by the observed changes in some key species. First, biomass, consumption, and mortality are compared among functional species-groups, key species, and aggregated species-groups (e.g., demersal fishes, commercial crustaceans) and then whole-system properties are compared. Finally, the effects of uncertainty on the model results are considered and some comparisons made with the earlier modelling efforts described above.

Methods

Ecopath (Polovina 1984; Christensen et al. 2000) is a simplified approach to ecosystem modelling. It models the whole ecosystem, with species aggregated into functional groups to make the model tractable (Appendix A, Table A1). Each group is represented by two linear equations, each of which must be balanced.

The first equation ensures balance among groups in the model:

$$(1a) \quad P_i = Y_i + B_i(M2_i + E_i + MO_i + \mathrm{BA}_i)$$

where, for group i, P_i is annual production, Y_i is annual catch, B_i is annual biomass, $M2_i$ is the total predation rate for group i, E_i is the net migration rate (emigration minus immigration), $MO_i = P_i(1 - \mathrm{EE}_i)$ is the "other mortality" rate, EE_i being "ecotrophic efficiency", and BA_i is the biomass-accumulation rate.

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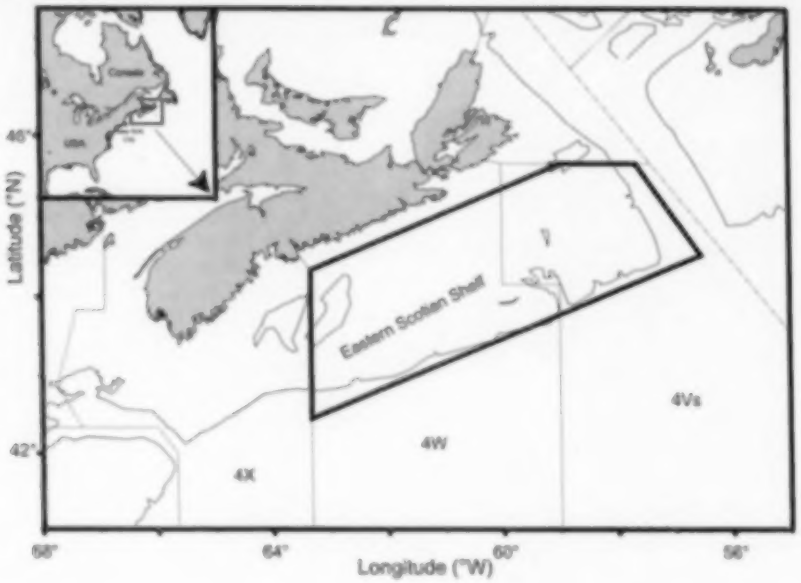
Fig. 1. Map of the Scotian Shelf, showing the eastern Scotian Shelf (NAFO Divisions 4VsW), outlined with a thick black line. The thin line represents the 200-m depth interval.



Equation 1*a* can also be expressed as

$$(1b) \quad B_i(P/B)_i\,EE_i - \sum_{j=1}^{n} B_j(Q/B)_j\,DC_{ji} - Y_i - B_iE_i - B_iBA_i = 0$$

where P/B is the ratio of production to biomass, Q/B is the ratio of consumption to biomass, and DC_{ji} is the fraction of the prey (i) in the diet of the predator (j) (Christensen and Pauly 1992).

The second equation, which balances the flows within each group, is

$$(2) \quad \text{Consumption} = \text{production} + \text{respiration} + \text{unassimilated food}$$

$$Q_i = P_i + R_i + GS_iQ_i$$

where, for group i, Q_i is consumption, R_i is respiration, and GS_i is the proportion of food that is not assimilated.

Other mortality

MO, other mortality, is expressed in Ecopath as $1 - EE_i$. In these terms, $1 - EE_i$ is the proportion of P_i that is not consumed by predators included in the model, nor caught by the fishery, nor accumulated in the system, so that

$$(3) \quad EE_i = (M2_i + Y_i)/P_i$$

Solving the model

The ecosystem is modelled using a set of simultaneous linear equations derived from the above relationships. Equation 1*b* is scaled by biomass. Thus, production and consumption are expressed as biomass ratios (P/B, Q/B). MO and $M2$ are annual mortality rates. Each group in the model is represented by the two balanced equations and requires six input parameters. Diet composition and catch (export) are mandatory and three of the other four parameters (B, P/B, Q/B, and EE) must be entered. The linear equations are solved and missing parameters estimated. (EE is estimated if all other parameters have been entered.) The most robust approach is to enter B, P/B, and Q/B where possible and allow the model to estimate EE. This provides an immediate check for mass balance because EE cannot be greater than 1. Sometimes it is necessary to enter EE, in which case a default value of 0.95 is used (Christensen and Pauly 1992).

Analysis of uncertainty

Mass-balance models are deterministic and require many input parameters, some of which may be poorly known, or adapted from other ecosystems or Ecopath models. This introduces a high level of uncertainty to the results of the model estimates. To explore the effects of uncertainty on the model results, two methods were used. The first is a simple sensitivity analysis (using a routine within Ecopath). Here, biomass, P/B, or Q/B is altered in 10% steps to plus or minus 50% to explore the impact on missing parameter estimates. Sensitivity to changes in diet, catch, or biomass accumulation (BA) cannot be explored using this method.

To explore the effects of uncertainty on the model results, a perturbation analysis was carried out once the Ecopath models were balanced, using the Autobalance routine (Kavanagh et al. 2004) and the Pedigree routine in Ecopath. The Autobalance routine randomly selects the initial input parameters from a predefined range of values using the Pedigree routine (see below). Thus, each run starts with a different set of conditions, and the routine searches for the combination that will produce a balanced model. A balanced model is defined as one where all groups have an EE of less

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than 1. In this case, the target EE was set to be 0.95. To reach this target the Autobalance routine was programmed to run for 10 000 runs.

Only the biomass and diet parameters can be directly perturbed in the Autobalance routine, thus it is not a full perturbation analysis. However, the Autobalance routine does allow *P/B* and *Q/B* to be "nudged" from their initial values during the run by predefined steps, in order to balance the model. In this case, *P/B* and *Q/B* were nudged in 10% steps: in practice, in some model balances *P/B* and *Q/B* were nudged and in others they are not, depending on the start conditions.

In the Pedigree routine, ranges of percent uncertainty are assigned to the biomass, *P/B*, *Q/B*, catch, and diet input or model estimates (model estimates have a high range of uncertainty). With this routine, the overall Pedigree of the model can be compared with that of other models (see Christensen et al. 2000). The Pedigree ranges are preset in Ecopath and values range between 10% and 80%, depending on the quality of the data. While this is not an empirical estimate of the uncertainty associated with the data, it is a step towards exploring the effects of uncertainty on model estimates. The Pedigree ranges were assigned to the two models using both the Ecopath criteria and the author's knowledge of the data (Appendix A, Table A2).

Thirty model runs were completed using the Autobalance routine, providing estimates of 95% confidence limits for all input and output parameters. This is especially useful for exploring the range of feasible solutions for groups with poor parameter estimates, e.g., seabird or shrimp biomass. When comparing the two models, a Mann–Whitney *U* two independent samples test was used to test whether differences between the models were significant, or an artefact created by the uncertainty of the input parameters. In some cases, a visual analysis using box-and-whisker plots was used to check whether differences detected by the Mann–Whitney test made sense ecologically. This, together with Bundy and Fanning (2005), constitutes the first uncertainty analysis of this type with an Ecopath model. It is preliminary, consisting of only 30 replicates, but it does provide some rigour for this type of comparative analysis.

Structure of the model

Species present on the eastern Scotian Shelf were aggregated into 39 groups (Appendix A, Table A3). There are 2 marine mammal groups, 1 seabird group, 24 fish groups, and 8 invertebrate groups, plus 2 zooplankton groups, phytoplankton and detritus. There are insufficient data to model the invertebrate groups in much more detail than is currently used.

Parameter estimation

Details of the methods and data for the parameter estimates for each group are given in Bundy (2004). The general approach is outlined below. Where possible, estimates were taken from the eastern Scotian Shelf for the specific time period of the model.

Biomass

Biomass of fish species was estimated from the RV groundfish survey adjusted for trawl catchability. Statistical analysis (*Z* test, using the mean of the annual mean catch per tow and their associated variance estimates for the two time periods, assuming that each year is an independent sample; Cochrane 1977) of the raw RV data indicates that the biomass of cod, silver hake (*Merluccius bilinearis*), haddock, American plaice (*Hippoglossoides plattesoides*), large halibut (*Hippoglossus hippoglossus*), skates (*Raja* spp.), flounders (Pleuronectidae), spiny dogfish (*Squalus acanthus*), redfish (*Sebastes* spp.), pollock (*Pollachius virens*), demersal piscivores, and demersal feeders decreased between the early 1980s and late 1990s: the biomass of small demersal feeders, small pelagics, capelin (*Mallotus villotus*), and northern sand lance (*Ammodytes dubius*; hereinafter sand lance) increased.

Approximate estimates of catchability for many species were available on a length basis, based on a meta-analysis of trawl survey estimates of catchability (Harley and Myers 2001; Harley et al. 2001). For species for which length-based catchability estimates were not available, an average catchability estimate was used for all length groups (Harley et al. 2001). A Student's *t* test of the *q*-adjusted mean biomass estimates from the RV survey was used to test whether there were differences between the two time periods for the *q*-adjusted large and small groups: estimates for large cod, large silver hake, large halibuts, large demersal piscivores, and large demersal feeders significantly decreased, whereas those for small cod, small silver hake, small demersal piscivores, and small demersal feeders did not; estimates for small halibut increased. Note that the *q*-adjusted biomass estimates for flounders, spiny dogfish, redfish, and pollock did not significantly decrease. For non-fish species a variety of survey data were used.

Biomass accumulation

BA was estimated from catchability-adjusted estimates of annual biomass. If there was an increase or decrease in biomass over the time period of either model, and if this formed part of a larger trend, BA was estimated as the slope of the regression for those years. For non-fish species other than grey seals, there were insufficient data to estimate BA, which may have led to incorrect estimates of unknown mortality or biomass and possibly an unbalanced model.

Production

Production in Ecopath is defined as "the elaboration of tissue (whether it survives or not) by a group over the period considered" (Christensen et al. 2000). It was assumed that the ratio of production to biomass is equivalent to total mortality, i.e., $Z = P/B$ (Allen 1971). Total mortality was estimated using catch curves and Paloheimo's method where possible. If data were not available for these methods, the empirical relationship $P = M \times B + C$, where M is natural mortality, B is biomass, and C is catch, was used. This was then expressed as *P/B*. It is necessary to assume a value for natural mortality, unless it is known. Where it was not possible to estimate *P/B*, values from the literature were used.

Consumption

Fish consumption for the late-1990s model was estimated from stomach-content data collected during RV surveys of the eastern Scotian Shelf during 1999 and 2000 (Laurinolli et al. 2004). Gastric-evacuation models, in conjunction with

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stomach-content data obtained from fish in the wild, were used to estimate total consumption and the proportions of the different prey consumed by fish predators to quantify feeding interactions among species. Gastric-evacuation rates were taken from the literature. Consumption rates per day were estimated for 5 cm length groups of fish, using the consumption model of dos Santos and Jobling (1995) based on experiments with cod (for details see Laurinolli et al. 2004). Consumption was then expressed as *Q/B* in the Ecopath model by dividing population consumption by population biomass.

For the early 1980s model, there were few consumption data for fish from the eastern Scotian Shelf. Where no estimates were available, estimates from the late-1990s model were used or estimates were taken from the literature.

Diet

Few empirical diet data were available for species from the eastern Scotian Shelf for the early-1980s period. The few exceptions include silver hake, grey seal, and pollock. Diet data were available for some species from surveys that took place on the Scotian Shelf from 1958 to 1969 and these were used in lieu of more recent data. For species for which no diet data were available from the eastern Scotian Shelf, diet estimates from the western Scotian Shelf and Georges Bank (J. Link, National Marine Fisheries Service, 166 Water Street, Woods Hole, MA 02543, USA, personal communication) or similar systems were used. These were adjusted for prey components where appropriate (i.e., prey in the diets that did not occur, or were uncommon, on the eastern Scotian Shelf were replaced by similar prey that do occur on the eastern Scotian Shelf). In the few cases with no diet information from any of these sources, diet data from the literature for similar systems were used.

For the late-1990s model, stomach-content data were available from research surveys conducted on the eastern Scotian Shelf in 1999 and 2000. Percent diet composition was estimated from the total consumption estimates described above (Laurinolli et al. 2004). All input data for the two models are given in Appendix B.

Balancing the early-1980s and late-1990s models

A key stage in developing mass-balance models is the process of fitting the data from different components of an ecosystem into one coherent picture, with flows that meet the mass-balance criteria. It should be an exercise in which information about the ecosystem is gained through this fitting process, for often a single-species view of the ecosystem (from which much of the input data are derived) does not reflect the multispecies world these species inhabit. Preconceived ideas may have to be revisited for these models to balance. For example, estimates of trawlable biomass, or estimates of consumption may be adjusted in order to balance the model.

Initially, neither the early-1980s nor the late-1990s model was balanced. The models were balanced using an iterative procedure, altering input parameters within the bounds of their estimated uncertainty. Three criteria were used to balance the models. (1) Key anchor groups were identified at each trophic level: grey seals (trophic level 4), large silver hake (trophic level 4), large cod (trophic level 4), haddock (trophic level 3), and small zooplankton (trophic level 2). The information was considered more certain for these groups than for other groups, and their parameters were altered as little as possible. In general, there was more certainty at higher than at lower trophic levels. (2). The five input parameters (biomass, *P/B*, *Q/B*, EE, and diet) had different degrees of uncertainty, depending on the functional groups that they represent. Generally, diet was the most uncertain, so this was often adjusted first. (3). For the fish species, the RV survey provides good estimates of the relative difference in fish biomass between the two time periods, and this is maintained for all species, except where noted. The changes to the model input parameters are detailed in Bundy (2004) and Appendix B.

Results

Biomass

The biomass estimates for some groups were adjusted during the balancing process. In particular, the biomass estimates for redfish and silver hake had to be revised downwards and those for small demersal feeders, squids, and shrimp upwards in both models in order for flows to balance. Sand lance biomass was increased in the early-1980s model and values for sand lance and small pelagics were decreased in the late-1990s model.

The biomass of many groups changed between the early 1980s and late 1990s. In addition to the changes noted above from the RV-survey data, Ecopath estimates indicate that the biomass of redfish, small demersal piscivores, small large demersal feeders, and small mesopelagics decreased between the two time periods, while the biomass of small crabs, shrimp, large zooplankton, and small zooplankton increased (Table 1).

When the species-groups were aggregated (Table 2), there was a significant decrease (Mann–Whitney test) in the biomass of demersal groundfish species and a significant increase in total biomass, grey seals, small pelagic species, commercial crustaceans, zooplankton, and phytoplankton. The increase in pelagic feeders and decrease in demersal feeders are reflected in a significant increase in the ratio of pelagic feeders to demersal feeders (for fishes only) from 0.3 to 3, which is an indicator of the negative effects of fishing (Zwanenburg 2000; Rochet and Trenkel 2003). The rationale is that as longer lived large demersal predators are removed by fishing, the abundance of short-lived small pelagics increases, owing to release from predation pressure.

Trophic structure

The trophic structure of the ecosystem changed between the two time periods. Biomass at all trophic levels significantly increased (Fig. 2*a*), and the composition of these trophic levels changed. The biomass increase at trophic level 4 was due to the increase in grey seal abundance and an increase in the number of other functional groups feeding at trophic level 4. In the early-1980s model, trophic level 4 was composed of four groups, transient pelagics, demersal piscivores, grey seals, and large halibut. In the late-1990s model, it was composed of eight groups with the addition of small demersal piscivores, dogfish, small halibut, and large cod. The total number of groups at trophic level 3 decreased by

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Table 1. Comparison of biomasses ($t \cdot km^{-2}$) in the early 1980s and late 1990s for groups whose biomass was estimated by the model or adjusted in the balancing process.

Ecopath group[a]	Early 1980s	Late 1990s	>20% change[b]	Mann–Whitney *U* test[c]
6. Large silver hake	0.80	0.33	↓	***
7. Small silver hake	**2.13**	**2.23**		***
15. Redfish	3.40	1.40	↓	***
19. Small demersal piscivores	0.11	0.08	↓	***
20. Large demersal feeders	0.10	0.05	↓	***
21. Small large demersal feeders	0.22	0.12	↓	***
22. Small demersal feeders	**0.26**	**0.78**	↑	***
24. Sand lance	**1.10**	**11.20**	↑	***
25. Transient pelagics	0.05	0.05		
26. Small pelagics	**1.22**	**8.50**	↑	***
27. Small mesopelagics	0.63	0.42	↓	***
28. Squids	0.66	0.53		***
30. Small crabs	**1.69**	**3.78**	↑	***
31. Shrimp	**2.77**	**13.57**	↑	***
36. Large zooplankton	**16.13**	**34.58**	↑	***
37. Small zooplankton	**34.00**	**44.00**	↑	***

[a]For scientific names see Table A1. Increased values are in boldface type.
[b]The arrows indicate whether or not changes were greater than 20%.
[c]Asterisks indicate that the Mann–Whitney *U* test was significant.

Table 2. Comparison of biomasses ($t \cdot km^{-2}$) of functional groups in the early 1980s and late 1990s.

Functional group	Early 1980s	Late 1990s	Percent change	Mann–Whitney *U* test[a]
Cetaceans and birds	0.24	0.27	13	
Grey seals	0.03	0.14	468	***
Demersal fish[b]	13.33	7.72	–42	***
Pelagic fish[c]	3.62	23.28	544	***
Commercial crustaceans[d]	4.60	17.66	284	***
Other invertebrates[e]	138.56	138.43	0	
Zooplankton	50.13	78.58	57	***
Phytoplankton	34.38	43.56	27	***
Total	244.89	309.65	26	***

[a]Asterisks indicate that the Mann–Whitney *U* test was significant.
[b]Cod (*Gadus morhua*), silver hake (*Merluccius bilinearis*), haddock (*Melanogrammus aeglefinus*), American plaice (*Hippoglossoides platessoides*), halibut (*Hippoglossus hippoglossus*, *Reinhardtius hippoglossoides*), flounders (Pleuronectidae), skates (*Raja* spp.), dogfish (*Squalus acanthus*), redfish (*Sebastes* spp.), pollock (*Pollachius virens*), demersal piscivores, large demersal feeders, and small demersal feeders.
[c]Transient mackerel (*Scomber scombrus*), capelin (*Mallotus villosus*), northern sand lance (*Ammodytes dubius*), transient pelagics (*e.g.*, tuna (*Thunnus* spp.), swordfish (*Xiphias gladius*), shark species), small pelagics (*e.g.*, herring (*Clupea harengus harengus*)), and small mesopelagics.
[d]Shrimp (*Pandalus* spp.), crabs (*eg.*, snow crab, *Chionoecetes opilio*).
[e]Squids (*Illex illecebrosus*, *Loligo pealeii*), echinoderms, polychaetes, bivalve molluscs, other benthic invertebrates.

four, and the increase in biomass at this trophic level was due to the increase in biomass of forage fish species. The increase in biomass at trophic level 2 was due to the increase in shrimp (*Pandalus* spp.) and large zooplankton.

Consumption

Annual consumption by each species-group increased or decreased in the same direction as biomass, with the exception of small mesopelagics and squids. Total consumption significantly increased, and this increase was greater than the increase in total biomass, perhaps because of the greater proportion of small individuals in the ecosystem in the late 1990s (Table 3).

When species-groups were aggregated into the larger functional groups (Table 4), consumption by grey seals, pelagic fish, commercial crustaceans, and zooplankton significantly increased from the early 1980s to the late 1990s. Consumption by demersal fish significantly decreased. When aggregated by trophic level, consumption significantly increased at trophic levels 2, 3, and 4 (Fig. 2*b*). Again these changes at the aggregate level mirror the changes observed for biomass.

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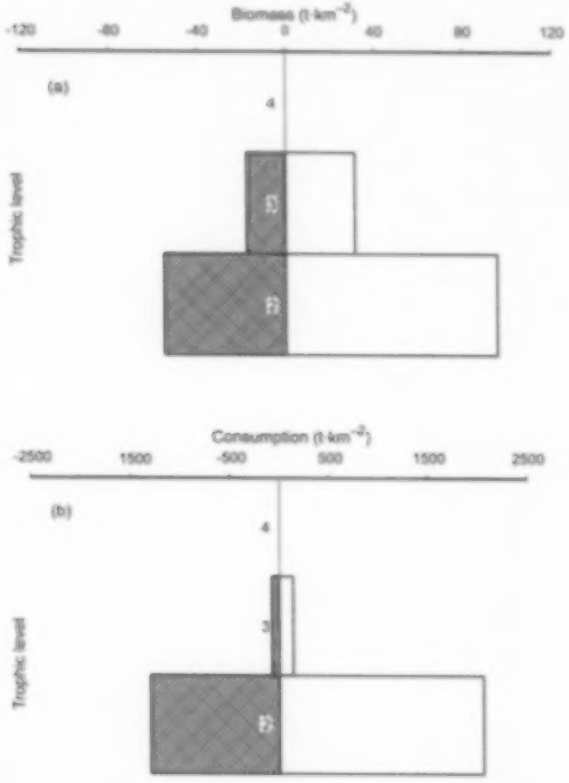
Fig. 2. Distribution of (*a*) biomass and (*b*) consumption by trophic level in the early 1980s (cross-hatched bars) and late 1990s (open bars). Early-1980s data are shown as negative for illustration purposes only. Trophic level 2 excludes the bivalves, echinoderms, polychaetes, and other benthic invertebrates, since their biomass did not change from one time period to the next. The increase in biomass at trophic levels 3 and 4 was significant at the 95% level.



Changes in mortality

Total mortality is an input parameter to the model for all groups (as *P*/*B*) and values are similar for many groups over the two time periods. There are no tests of significance associated with total mortality, since this parameter was secondarily perturbed in the uncertainty analysis if it was necessary to balance the models. Where there are differences, (e.g., for large silver hake, haddock, demersal piscivores), these are based on empirical estimates of Z, or, as in the case of sand lance, on assumptions about relative productivity in the two time periods (Bundy 2004). For small cod, total mortality was higher in the late 1990s than in the early 1980s, based on estimates of productivity obtained by sequential population analysis.

Total mortality is composed of four components in the models: fishing mortality, predation mortality, loss (or gain) due to BA, and "other mortality". Other mortality may be due to disease, senescence, and environmental effects, but is treated as unexplained mortality in these models. The distribution of mortality by fish group changed from the early 1980s to the late 1990s (Fig. 3).

Fishing mortality

For the traditional commercial species such as cod, haddock, and flounders, there was a significant reduction in fishing mortality from the early 1980s to the late 1990s, as expected given the moratorium on fishing for groundfish on the eastern Scotian Shelf. Fishing mortality of nontraditional species such as large demersal piscivores and large crabs (not shown) significantly increased. Fishing mortality of large silver hake significantly decreased, but fishing mortality of small silver hake increased slightly. Note that catch was not perturbed directly in the uncertainty analysis, thus the results of the significance tests reflect variation in biomass, not uncertainty in the catch.

Predation mortality

Predation mortality of species such as cod (large and small) and haddock significantly increased over the two time periods. As the biomass of these groups decreased from early 1980s to late 1990s, predation was a greater source of mortality in the more recent period.

Predation mortality of small cod was estimated to account for 97% of the total mortality in the late 1990s. In the early-1980s model, large cod, demersal piscivores, and grey seals were the main predators of small cod (Fig. 4*a*). In the late 1990s, the main predators were similar, but also included silver hake, squids, and cetaceans. The large increase in estimated predation mortality was not due to increased consumption of small cod (consumption of small cod decreased from 35 000 to 13 200 t·year^{-1}), but to the large decrease in biomass of small cod. Thus, although less small cod was consumed, predation had a larger impact on the greatly reduced biomass.

Predation mortality of large cod also significantly increased, but was estimated to constitute only 5% of the total mortality in the late 1990s. The main predators during both time periods were grey seals, dogfish, and demersal piscivores (Fig. 4*b*). The increase in predation mortality was due to grey seals, although estimated consumption of cod by grey seals decreased from 393–654 t·year^{-1} year in the early 1980s to 90–214 t·year^{-1} in the late 1990s. Thus, predation had a large impact on large cod, owing to their low biomass, which is analogous to the situation for small cod.

Predation mortality of haddock was estimated to have increased because of the increased consumption of haddock by pollock and silver hake, despite a decrease in consumption by most other predators (Fig. 4*c*). In the early 1980s, cod, haddock, pollock, and grey seals were the main predators of haddock, whereas in the late 1990s, pollock and silver hake were the dominant predators, likely feeding on the abundant 1998 and 1999 haddock year classes.

For other groups, predation mortality in the model significantly decreased, for example, for large and small silver hake, small halibut, and the forage fish species. In the case of small pelagic feeders and small demersal feeders, this decrease was significant. For the larger fish, such as silver hake, biomass decreased and the reduction in predation mortality was presumably caused by a decrease in total consumption. Total consumption decreased because of a decrease in

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Table 3. Comparison of consumption ($t \cdot km^{-2}$) in the early 1980s and late 1990s.

Ecopath group[a]	Early 1980s	Late 1990s	>20% change[b]	Mann–Whitney *U* test[c]
1. Cetaceans	2.33	2.66		
2. Grey seals	0.30	**1.68**	↑	***
3. Seabirds	0.66	0.66		
4. Large cod	2.56	0.14	↓	***
5. Small cod	3.80	0.48	↓	***
6. Large silver hake	5.92	1.81	↓	***
7. Small silver hake	16.57	12.93	↓	***
8. Haddock	3.36	1.98	↓	***
9. American plaice	1.29	0.72	↓	***
10. Large halibut	0.08	0.04	↓	***
11. Small halibut	0.04	**0.28**	↑	***
12. Flounders	1.76	1.80		
13. Skates	0.52	0.18	↓	***
14. Dogfish	0.48	0.21	↓	***
15. Redfish	6.80	2.80	↓	***
16. Pollock	2.93	1.33	↓	***
17. Transient mackerel	1.30	0.47	↓	***
18. Large demersal piscivores	0.60	0.14	↓	***
19. Small demersal piscivores	0.59	0.41	↓	***
20. Large demersal feeders	0.24	0.09	↓	***
21. Small large demersal feeders	1.04	0.48	↓	***
22. Small demersal feeders	1.11	**3.33**	↑	***
23. Capelin	0.13	**19.37**	↑	***
24. Sand lance	8.46	**45.58**	↑	***
25. Transient pelagics	0.09	0.09		
26. Small pelagics	5.58	**39.10**	↑	***
27. Small mesopelagics	3.15	2.11	↓	
28. Squids	2.92	2.34		
29. Large crabs	0.18	**0.37**	↑	***
30. Small crabs	2.53	**5.67**	↑	***
31. Shrimp	31.26	**153.36**	↑	***
32. Echinoderms	426.79	426.79		
33. Polychaetes	330.82	330.82		
34. Bivalve molluscs	446.44	446.44		
35. Other benthic invertebrates	61.25	61.25		
36. Large zooplankton	314.55	**674.24**	↑	***
37. Small zooplankton	952.00	**1232.00**	↑	***
Total	2640.44	**3474.16**	↑	***

[a]For scientific names see Table A1. Increased values are in boldface type.
[b]The arrows indicate whether or not changes were greater than 20%.
[c]Asterisks indicate that the Mann–Whitney *U* test was significant.

Table 4. Comparison of consumption ($t \cdot km^{-2}$) of functional groups in the early 1980s and late 1990s.

Functional group[a]	Early 1980s	Late 1990s	Percent change	Mann–Whitney *U* test[b]
Cetaceans and birds	2.99	3.32	10.77	
Grey seals	0.30	1.68	468.00	***
Demersal fish	49.69	29.15	–41.33	***
Pelagic fish	18.72	106.73	470.18	***
Commercial crustaceans	33.97	159.40	369.17	
Other invertebrates	1268.22	1267.65	–0.05	***
Zooplankton	1266.55	1906.24	50.51	***
Total	2640.44	3474.16	31.58	***

[a]See Table 2 for species composition of groups.
[b]Asterisks indicate that the Mann–Whitney *U* test was significant.

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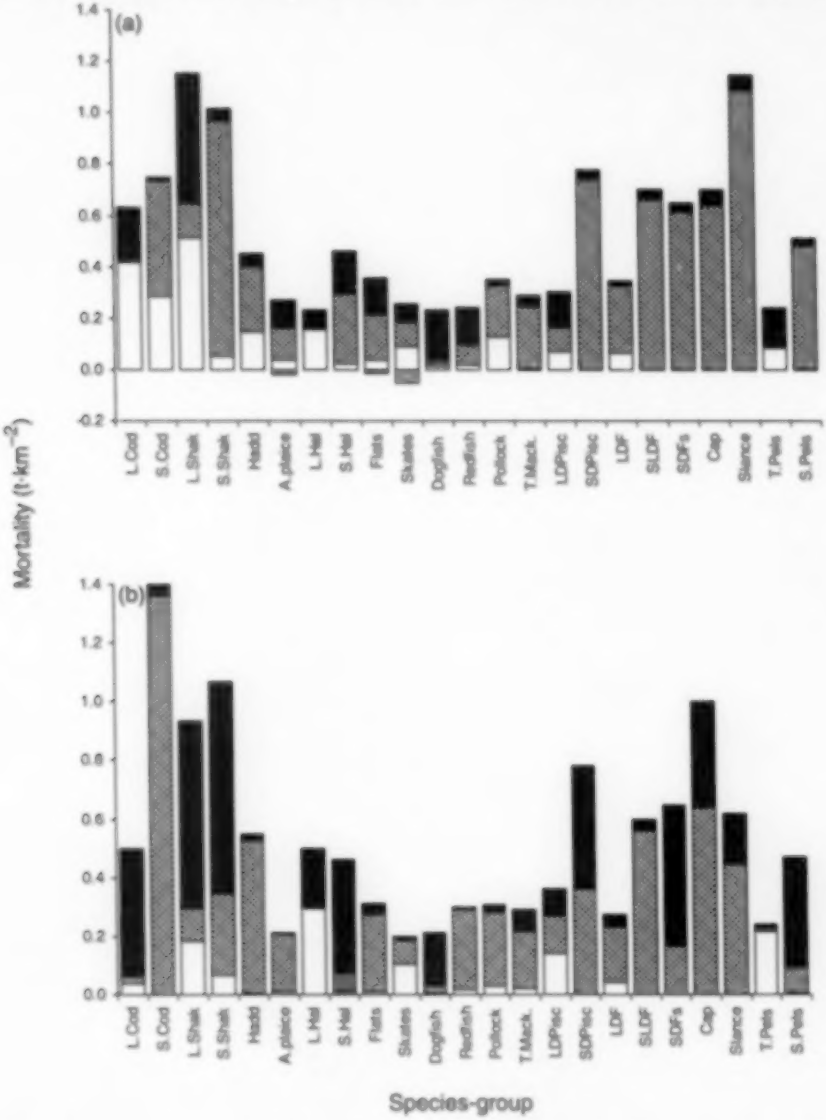
Fig. 3. Distribution of fishing (*F*, open bars), predation (*M2*, cross-hatched bars), biomass accumulation (BA, shaded bars), and other mortality (*MO*, solid bars) over fish species in (*a*) early-1980s and (*b*) late-1990s models. See Table A1 for species-group names.



predation by dogfish and demersal piscivores and cannibalism, although predation by grey seals and transient pelagic feeders increased (Fig. 5*a*).

In the case of the forage fishes (small demersal feeders, sand lance, and small pelagics), and small crabs (not shown), the decrease in predation mortality resulted from the large estimated increases in their biomass, and a decrease in the biomass of some of their predators. Total consumption of each of these groups significantly increased from the early 1980s to the late 1990s.

Consumption of sand lance increased from 123 000 t·year^{-1} in the early 1980s to 509 000 t in the late 1990s. Their main predators in the early 1980s were cod, haddock, cetaceans, and pollock, whereas in the late 1990s, their main predators were small demersal feeders, small silver hake, and grey seals (Fig. 5*b*).

Shrimp have a wide range of predators, which consumed 457 000 t of shrimp per year in the early 1980s and over 2 000 000 t the of shrimp in the late 1990s. In the early 1980s their main predators were redfish, small silver hake, and small cod, whilst in the late 1990s they were small silver hake, sand lance, and capelin, all of whose biomass is large in this time period (Fig. 5*c*).

Other mortality

There were significant increases in other mortality for several groups, the most notable being large cod, large and small silver hake, small halibut, small demersal piscivores,

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Fig. 4. Box-and-whisker plot comparing predation mortality on (*a*) small cod (*Gadus morhua*), (*b*) large cod, and (*c*) haddock (*Melanogrammus aeglefinus*) in the early 1980s (shaded bars) and late 1990s (open bars). Horizontal lines represent the median, the boxes represent 50% of the values, and the whiskers extend to the highest and lowest values (excluding outliers). See Table A1 for species-group names.

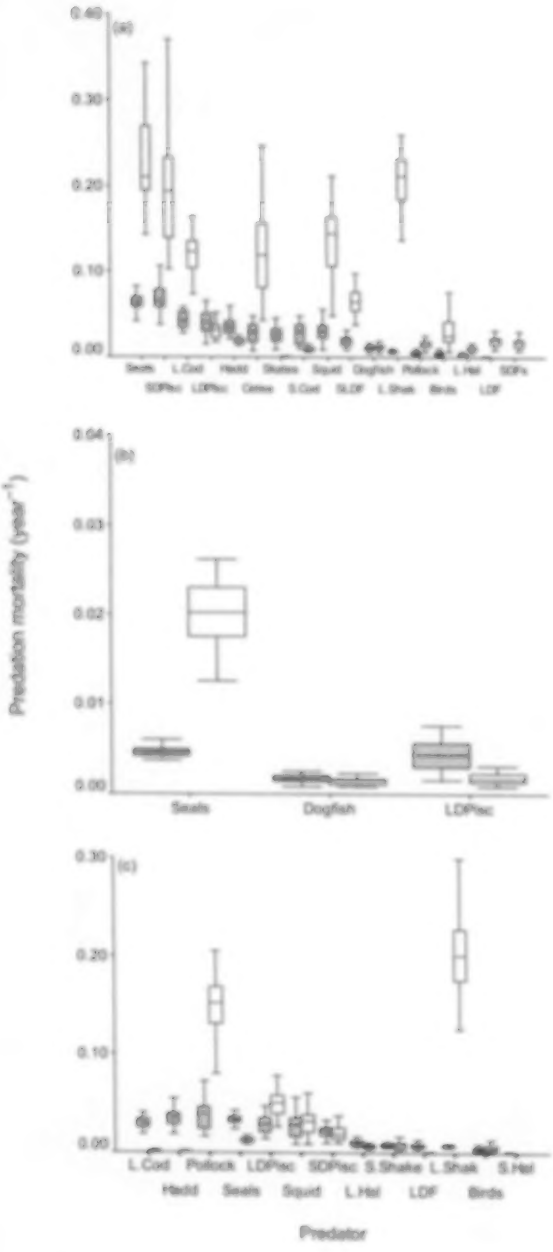

Fig. 5. Box-and-whisker plot comparing predation mortality on (*a*) silver hake (*Merluccius bilinearis*), (*b*) northern sand lance (*Ammodytes dubius*), and (*c*) shrimp (*Pandalus* spp.) in the early 1980s (shaded bars) and late 1990s (open bars). Horizontal lines represent the median, the boxes represent 50% of the values, and the whiskers extend to the highest and lowest values (excluding outliers).

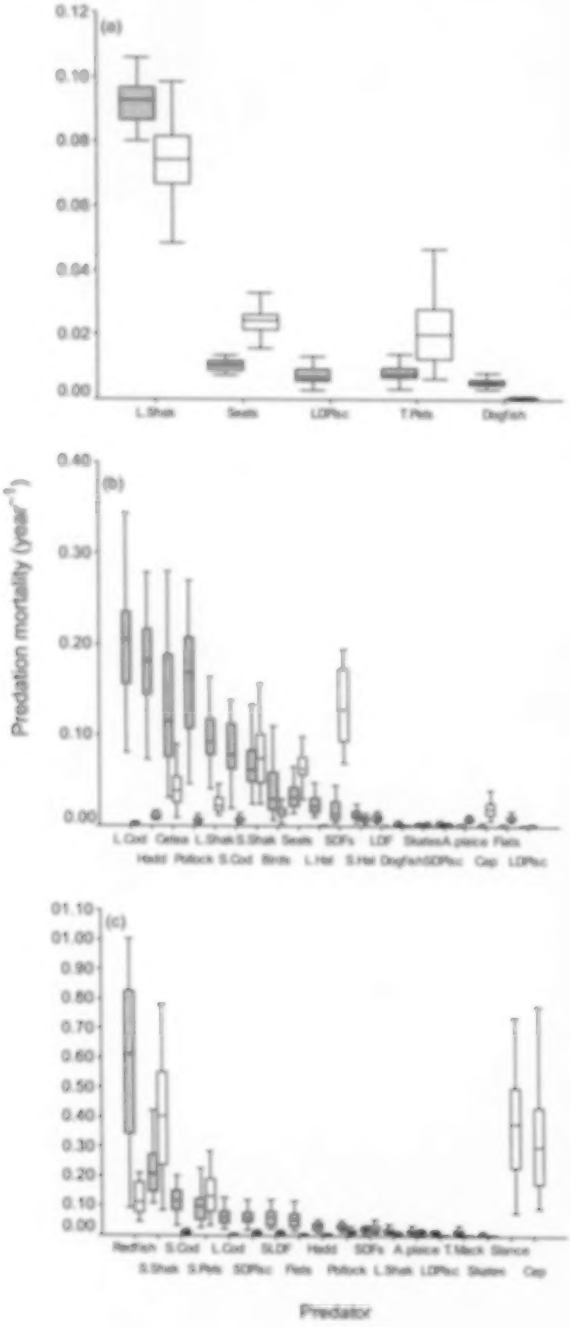

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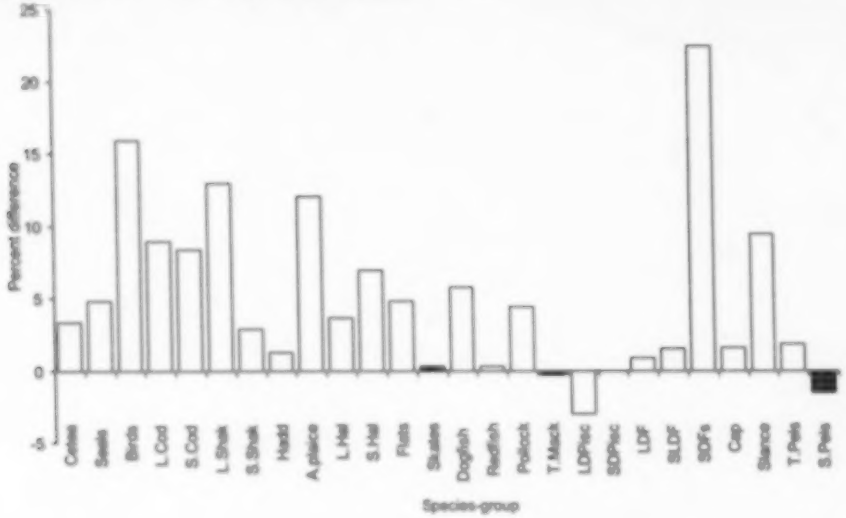
Fig. 6. Percent differences in trophic level from the early 1980s to the late 1990s. Shaded bars denote species-groups for which changes were not significant. See Table A1 for species-group names.



small demersal feeders, capelin, sand lance, and small pelagics (Fig. 3).

Trophic level

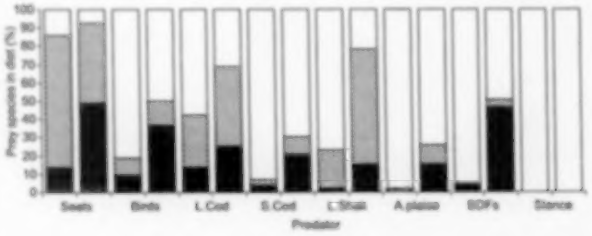
The average trophic level at which feeding occurs significantly increased for many groups from the early 1980s to the late 1990s (Fig. 6), although groups at the lower trophic levels, such as the invertebrates, squids, and mesopelagics showed no change. This increase in trophic level may indicate an increase in piscivory or an increase in the consumption of prey with increased trophic level, such as small demersal feeders and sand lance, or both. To disentangle these effects, the diets of eight groups with significant increases in their trophic level were examined for relative changes in the proportion of small demersal feeders, sand lance, fish, and other prey species (Fig. 7). For all groups except sand lance there was an increase in both the proportion of fish eaten and the proportion of sand lance eaten. Indeed, with the exception of haddock, pollock, and transient mackerel (*Scomber scombrus*), the increase in fish consumption was due to an increase in sand lance consumption.

The trophic level of small demersal feeders increased because longhorn sculpin (*Myoxocephalus octodecemspinosus*), 66% of whose diet consists of fish (including sand lance), constituted a larger proportion of the biomass of this group in the late 1990s than in the early 1980s. The trophic level of sand lance increased because they ate significantly more large zooplankton in the late 1990s than in the early 1980s. Although the late-1990s sand lance diet was estimated using data from the eastern Scotian Shelf, the early-1980s diet was estimated using data from Georges Bank (see Bundy 2004, appendix 2, table 24), so this conclusion is weakly supported.

Changes in predator structure

In addition to the general increase in piscivory, the predator structure of the eastern Scotian Shelf has also changed since the early 1980s (Table 5). During the early 1980s, cod

Fig. 7. Percentages of small demersal feeders (shaded bars), sand lance (solid bars), other fish (cross-hatched bars), and other prey (open bars) in the diet of groups with significantly increased trophic levels in the early-1980s (first bar) relative to the late-1990s (second bar) balanced models. Non-open bars represent the total percentage of fish in the diet. See Table A1 for species-group names.



was the main predator of fish and commercial invertebrates in the ecosystem. Other important predators included demersal piscivores (large and small) and silver hake. However, in the late 1990s, cod predation was minimal, whereas grey seals and silver hake (large and small) were the main predators of fish and commercial invertebrates. Biomass of, and consumption by, grey seals increased and they became the main predator of fish. However, though biomass of, and consumption by, large silver hake have decreased, it remains an important predator of capelin and small pelagics, as well as pollock, haddock, small cod, and silver hake. Small demersal feeders also appear to be the main predators of sand lance and small crabs, owing to the increase in biomass of longhorn sculpin. Capelin and sand lance were important predators of shrimp in the early 1990s.

Ecosystem statistics

Total system throughput is the overall size of the system and is the sum of consumption, exports, respiratory flows,

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Table 5. Predator structure in the Ecopath model.

	Predator										
Prey	Cetea	Seals	Birds	L.Cod	S.Cod	L.Shak	S.SHake	Hadd	A.plaice	L.Hal	S.Hal
(A) Early 1980s											
Large cod		1									
Small cod	0	1	0	3	0	0		0		0	
Silver hake		0				1					
Small silver hake	0	0		0	0	1	0	0	0	0	0
Haddock		0	0	1		0	0	2		0	0
American plaice		0		0	0			0	0	0	0
Flounders		0		3				0	0	0	0
Skates		0								0	
Redfish	0	0		3	0	0		0	0		0
Pollock		0		2	0	1	0				
Small demeral piscivores	0	0		1	0					0	
Small LDFs	0	0		1	0			0	0	0	0
Small demersal feeders		0	0	2	0	0	0	3	0		0
Capelin		0		0	0	0	0		0		0
Sand lance	3	0	0	1	0	0	0	2	0	0	0
Small pelagics	2	0	0	3	0	0	0	0	0	0	0
Small crabs		0	0	1	3		0	0	0	0	0
Shrimp		0	0	0	3	0	2	0	0	0	0
(B) Late 1990s											
Large cod		1									
Small cod	0	1	0	0	0	3		0		0	
Silver hake		2				1					
Small silver hake	0	0		0	0	3	1	0	0	0	0
Haddock		0	0	0		1	0	0		0	0
American plaice		1		3	0			0	0	0	0
Flounders		1		0				0	0	0	0
Skates		1								2	
Redfish	0	2		0	0	0		3	0		0
Pollock		0		0	0	3	1				
Small demeral piscivores	2	3		0	0					0	
Small LDFs	0	1		0	0			0	0	0	0
Small demersal feeders		1	0	0	0	0	0	0	0		0
Capelin		3		0	0	1	0		0		0
Sand lance	1	3	0	0	0	0	2	0	0	0	0
Small pelagics	3	0	0	0	0	2	0	0	0	0	0
Small crabs		2	0	0	0		0	0	0	0	0
Shrimp		0	0	0	0	0	1	0	0	0	0

Note: For each prey in the left-hand column, the top three predators are marked in the rows. Other predators are indicated by a zero. See Table A1 for

and flows to detritus. Increases in the sum of consumption and exports were counterbalanced by a significant decrease in the sum of all flows to detritus (and a decrease in the sum of respiratory flows), resulting in no net difference in the size of these systems (Table 6). There was also no difference in the sum of all production, net system production, or calculated primary production. There was a significant increase in total biomass and in total biomass / total throughput.

One of the most striking declines is the decrease in the total catch, the gross efficiency of the catch, and the mean trophic level of the catch (significant). Thus, the biomass and trophic level of the catch were lower in the late 1990s than in the early 1980s, yet more primary production was required to produce it. This analysis can be taken further by examining the trend in total annual catch and average trophic level of the catch since 1960 (Fig. 8). The average trophic level of the catch was relatively stable at an average of 3.6 until the late 1980s, when it began to decline, reaching a low of 2.8 in 1999. Total catch from the eastern Scotian Shelf also declined.

Uncertainty analysis

The results of the sensitivity analysis indicated that few functional groups exert a large influence on the parameter estimates for other groups. In the early 1980s, these groups were small silver hake (sensitive groups were large zooplankton, small zooplankton, and small mesopelagics), small demersal piscivores (sensitive groups were large crabs and flounders), small mesopelagics (sensitive groups were squids), and large zooplankton (sensitive groups were small zooplankton). In each case, a –50% change in the input parameter produced a 40% or greater change in the estimated

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Flats	Skates	Dogfish	Redfish	Pollock	T.Mack.	LDPisc	SDPisc.	LDF	SLDF	SDFS
		0				1				
	0	0		0		0	2	0	0	0
		0				0				
	0	0		2		3	0	0		0
				3		0	0	0		
		1				0	3	0	2	
	0	2		0		0	1			0
	0					0		0		
0	0			2		1	0	0	0	0
				0		0	0	0	0	0
		0				3				
	3	3				2	0	0		0
0	1	0				0	0	0	0	0
0	0									0
0	0	0		0		0	0	0		0
	0	0		0	1	0	0	0		0
0	2	0		0		0	0	0	0	0
0	0	0	1	0	0	0	0	0	0	0
		0				0				
	0	0		0		0	2	0	0	0
		0				0				
	0	0		0		0	0	0		0
		0		2		3	0	0		
		2				0	0	0	0	
	0	0		0		0	2			3
	0					0		0		
0	0	0	0	1		0	0	0	0	0
				0		0	0	0	0	0
		0				0				
	0	0				0	3	0		0
0	0	0	3			0	0	0	0	2
0	0									0
0	0	0	0	0		0	0	0		1
	0	0		1	0	0	0	0		0
0	0	0		0		0	0	0	0	1
0	0	0	2	0	0	0	0	0	0	0

species-group names.

parameter for each of the groups in parentheses. In the late-1990s model, large zooplankton again exerted a strong influence on small zooplankton, and small mesopelagics on squids. However, squids (small demersal piscivores) and transient pelagic species (dogfish) were the only other groups to which other groups were hypersensitive. Small silver hake was still influential in the late-1990s model, but less so.

All the groups had a high degree of sensitivity to their own input parameters (with the exception of the cetaceans, whose missing parameter, EE, is zero). In the early-1980s model, the most sensitive groups were small silver hake, large zooplankton, and small mesopelagic species. In the late-1990s model, the most sensitive groups were large zooplankton and small mesopelagics. The biomass of small silver hake is not well estimated, even with q-correction. Given the sensitivity of other groups to small silver hake in the early-1980s model, and its autosensitivity, it is important to be able to describe this group better.

Discussion

The collapse of the groundfish stocks and the subsequent increase in invertebrate and forage fish abundance had little significant effect on the eastern Scotian Shelf ecosystem when measured at the whole-ecosystem level: few of the whole-system indices examined changed. Given the number of parameters and their associated uncertainty required to estimate these indices, this result is perhaps not surprising.

The major changes in the ecosystem properties of the eastern Scotian Shelf were observed in the fishery indices.

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Table 6. Comparison of system statistics for the early-1980s and late-1990s models.

	Early 1980s	Late 1990s	>20% change[a]	Mann–Whitney test[b]
Sum of all consumption ($t \cdot km^{-2} \cdot year^{-1}$)	**2640**	**3474**	↑	***
Sum of all exports ($t \cdot km^{-2} \cdot year^{-1}$)	5.27	1.79	↓	
Sum of all respiratory flows ($t \cdot km^{-2} \cdot year^{-1}$)	2776	2273		
Sum of all flows into detritus ($t \cdot km^{-2} \cdot year^{-1}$)	2247	1375	↓	***
Total system throughput ($t \cdot km^{-2} \cdot year^{-1}$)	7669	7124		
Sum of all production ($t \cdot km^{-2} \cdot year^{-1}$)	3241	2904		
Mean trophic level of the catch	3.54	3.24		***
Gross efficiency (catch/net primary production)	0.00062	0.00021	↓	***
Calculated total net primary production ($t \cdot km^{-2} \cdot year^{-1}$)	2776	2274		
Total primary production / total respiration	1	1		
Net system production ($t \cdot km^{-2} \cdot year^{-1}$)	0.35	0.62	↑	
Total primary production / total biomass	11.34	7.34	↓	***
Total biomass / total throughput	**0.032**	**0.043**	↑	***
Total biomass, excluding detritus ($t \cdot km^{-2}$)	**245**	**310**	↑	***
Total catches ($t \cdot km^{-2} \cdot year^{-1}$)	1.73	0.49	↓	

Note: Units are as shown, or dimensionless. Increased values are in boldface type.
[a]The arrows indicate whether or not changes were greater than 20%.
[b]Asterisks indicate that the Mann–Whitney *U* test was significant.

Fig. 8. Average trophic levels of the catch. Trophic levels are derived from Ecopath models. The broken line represents the average trophic level of the catch when the trophic level based on estimates from the early-1980s model is used for 1960–2000. The solid line represents the average trophic level of the catch when trophic-level estimates from the early 1980s are used for 1960–1992 and trophic-level estimates from the late-1990s model are used for 1993–2000.

Two indices, the average trophic level of the catch and the ratio of pelagic feeders to demersal feeders, reflected the marked effect of fishing on the ecosystem. The eastern Scotian Shelf exhibits the classic symptoms of fishing down the food web, which occurs when the average trophic level of the catch declines over time, with a concurrent decrease in the total catch (Pauly et al. 1998, 2001). Both the average trophic level and the catch have decreased since the early 1990s. Lower trophic levels are generally more productive than higher trophic levels and as an ecosystem is fished down, the catch can remain high. When the catch also decreases, this may indicate that the production of the whole system is low. On the eastern Scotian Shelf, a vacuum has been created at the higher trophic levels of the ecosystem, and the fishery is steadily fishing down the food web.

At a less aggregated level, the model indicates that there were substantial changes in the ecosystem, even allowing for uncertainty in the estimates. For the first time the size ($t \cdot km^{-2}$) of the whole eastern Scotian Shelf ecosystem was estimated, albeit an approximation with associated uncertainties. Biomass and consumption increased at all trophic levels, and for all functional groups, with the exception of the demersal feeders and other invertebrates. Despite the general increase, the total size of the system (total throughput) did not increase, owing to reduced flow to detritus and reduced respiration. This indicates that the system may have been more efficient in the late 1990s than in the early 1980s, as suggested by the higher cycling index and mean path length (not shown). The greatest change in the ecosystem is the switch from a demersal-feeder-dominated system to a pelagic-feeder-dominated system, indicating a shift in trophic flow from the demersal to the pelagic side of the food web. Average trophic level and piscivory increased and the predator structure changed: in the early-1980s model, cod was the most important predator, and its role as a predator in the ecosystem was reasonably well defined, whereas in the late-1990s model, cod was relatively minor component in a productive ecosystem, dominated by pelagics, forage fish, and invertebrates.

These results contrast with those for the Newfoundland–Labrador ecosystem (Sheila Heymans, Fisheries Centre, University of British Columbia, Vancouver, BC V6T 1Z4, Canada, unpublished data) and the northern and southern Gulf of St. Lawrence ecosystems (Lyne Morissette, Fisheries Centre, University of British Columbia, unpublished data), which share broad similarities in their changes before and after the collapse of the groundfish stocks. S. Heymans concluded that the Newfoundland–Labrador ecosystem became more stressed after the collapse of the cod stocks, and the total size of the system decreased. L. Morissette found a significant decrease in many of the ecosystem properties in the northern Gulf of St. Lawrence and an increase in the southern Gulf of St. Lawrence. As on the eastern Scotian Shelf,

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the abundance of seal species increased, the abundance of large demersal fish decreased, and the abundance of shrimp and crabs increased in some ecosystems; this was coupled with a decrease in the average trophic level of the catch. However, the biomass of forage fish species did not significantly increase. These differences in response may help solve the enigma concerning the lack of recovery of cod stocks in these ecosystems. The large biomass of forage fish on the eastern Scotian Shelf, for example, may be impeding the recovery of cod because the forage fish prey on small cod or compete with them for food (Bundy and Fanning 2005).

Although it was known from RV surveys that the biomass of sand lance, capelin, and small pelagics (herring) had increased on the eastern Scotian Shelf, their biomass was poorly estimated by the RV trawl survey and there were no estimates of absolute biomass. By incorporating estimates of sand lance, capelin, and herring biomass, adjusted for catchability, into the Ecopath model, constraints have been placed on biomass estimates. For example, Ecopath estimates of sand lance biomass, incorporating uncertainty, range from 22 000 to 195 000 t in the early-1980s model and from 517 000 to 1 712 000 t in the late-1990s model. These values do not agree with previous, but largely unsupported, notions of what the sand lance biomass might be, and though these ranges are wide, they are more realistic than the RV estimates of 54 and 11 452 t for the respective time periods.

In general, the Ecopath results support those of earlier efforts to model the Scotian Shelf. Mills (1980) proposed that there was less energy on the Scotian Shelf than in other northwest Atlantic ecosystems and suggested three hypotheses to explain this. His first hypothesis, that primary production on the Scotian Shelf might be underestimated, has some support. The estimates of primary production used here are three times higher than those used by Mills and Fournier (1979). However, continuous plankton recorder (CPR) data indicate that phytoplankton has increased since the 1960s (Sameoto 2004). Mills' (1980) second hypothesis was that the transfer efficiency assumed (10%) might be too low. The transfer efficiencies in the two models presented here were between 13% and 20% for trophic levels 2–4, therefore 10% may be too low. The third hypothesis — that the food chain may be shorter than in other ecosystems — was negated by Mills et al. (1984), who used ^{13}C as a tracer to study food-web structure on the Scotian Shelf. Their results indicated that food chains on the Scotian Shelf were 4 or 5 steps long, which is similar to those in other areas. The mean path length in the two Ecopath models presented here was around 3 steps, fewer than the 4 or 5 estimated by Mills et al. (1984). Sinclair et al. (1984) revisited these earlier models and concluded that more rigorous estimates of fish biomass and production were required in order to establish higher constraints at higher trophic levels: 20 years later the same conclusion has to be drawn, except that it would be extended to include the benthic and zooplankton groups. There is still uncertainty concerning input data, as revealed by the unknown mortality terms in the Ecopath models.

Information from estimates of other mortality

There are large other or unknown mortality estimates for several groups. The extent of this mortality is dependent on the input parameters *P/B* and biomass, and the levels of fishing and predation mortality experienced by each group (catch, diet, and consumption by predators) and the BA term. The other mortality term is informative, for it indicates an information gap in one or more of these parameters.

Large silver hake have a large estimate of other mortality in both models. The silver hake biomass estimates are uncertain, ranging from 81 000 to 191 000 t in the early-1980s model. Ultimately, the lower end of the range of biomass estimates was used in both models for large silver hake. However, the *P/B* estimates for silver hake are among the highest for the fish groups (Appendix B). These are based on the premise that $Z = P/B$ and are based on estimates of Z. It is likely that Z has been greater than *P/B* for large silver hake since the early 1980s because their biomass has decreased. Small silver hake also has a large other-mortality term in the late-1990s model. In the early-1980s model, cannibalism and predation by large cod were important sources of mortality. These are much reduced in the late-1990s model, but the biomass of small silver hake has remained relatively constant. If total mortality is as high as estimated, then a large part of this mortality remains unexplained. A confounding factor when modelling silver hake is that the stock is not confined to the model area: its distribution extends over the whole of the Scotian Shelf, and also into deeper waters off the shelf edge. It is thus possible that the model is failing to capture a source of mortality that occurs outside the model area, or that the biomass or productivity in the area has been incorrectly estimated.

Perhaps the most puzzling large other-mortality term is the estimate for large cod. In the early-1980s model, this accounted for about 30% of total mortality; in the late-1990s model, it increased to 88%. Thus, almost all the mortality of large cod is not explained in the late-1990s model. In the early-1980s model, the unaccounted-for mortality may be due to inaccuracy in the actual amount of cod removed by harvesting (e.g., unrecorded, under-recorded, and misreported catches). Since 1993 there has been no fishery for cod on the eastern Scotian Shelf, although there is a small by-catch in the halibut fishery. Fishing mortality is unlikely to account for the unexplained mortality of large cod in the late 1990s, unless there is some transport of eastern Scotian Shelf cod to the western Scotian Shelf. The groundfish fishery in the adjacent western Scotian Shelf may take some eastern Scotian Shelf cod if this occurs. Few predators of large cod were identified. Grey seals have been implicated as a source of mortality of cod, especially since the collapse of the cod stock, but available data do not substantially support this hypothesis (Bundy and Fanning 2005). Furthermore, the actual total mortality, Z, of large cod during the late 1990s is higher than 0.5·year^{-1} — it was estimated at 1.04·year^{-1}. This was reduced in balancing the model, because such a high estimate created an impossibly large respiration to biomass ratio and *P/Q* (Bundy 2004). Thus, for large cod, the total estimated mortality is twice the production, so unless mortality is reduced, this population will continue to decline.

The high mortality estimates, particularly in large cod, are problematic and are common to many Canadian east coast cod stocks, with the exception of those in North Atlantic Fisheries Organisation Division 4X (e.g., Chouinard et al. 2002; Smedbol et al. 2002; Dutil et al. 2003). Modelling the

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Table 7. Comparison between estimates of Ecopath and shrimp-trawl biomass for the early 1980s and late 1990s.

	Early 1980s	Late 1990s	Percent difference
Estimated shrimp-trawl biomass (t·km^{-2})	0.102	0.201	197
Estimated Ecopath biomass (t·km^{-2})	2.77	13.57	490
Percent difference	2713	6752	

ecosystem with Ecopath has not helped to explain the high cod mortality, although more information on predators of large cod could change this.

Uncertainty at lower trophic levels

Another specific concern with the two models developed here are the large biomass estimates at the lower trophic levels, particularly shrimp, and the increase in the biomass of the two zooplankton groups between the two model periods. Shrimp biomass was estimated by the Ecopath model in both time periods because the original input estimates from shrimp trawl surveys were too low (i.e., EE was greater than 1). When these are compared, the differences between the Ecopath estimates and those based on shrimp-trawl surveys are large (Table 7). Clarifying the uncertainty associated with both the shrimp-trawl and the Ecopath estimates of biomass may make these estimates more comparable.

The shrimp trawl only estimates the biomass of northern shrimp, *Pandalus borealis*, whereas the shrimp group in the model includes all shrimp species present on the eastern Scotian Shelf. To account for this, the trawl survey estimates were adjusted upwards by 25%. However, this may be too low, and in addition the catchability of *P. borealis* to the trawl is likely to be less than 1. The Ecopath estimate of biomass is derived from the consumption of shrimp by their predators. The main predators of shrimp are redfish, small silver hake, small cod, small pelagics, and large cod in the early-1980s model, and small silver hake, sand lance, and capelin in the late-1990s model. With the exception of large cod in the early-1980s model, these are all groups for which high uncertainty is associated with their biomass estimates and diets. This uncertainty is transferred to uncertainty in the biomass estimates for shrimp.

There have been no systematic surveys of large zooplankton on the Scotian Shelf, with the exception of the CPR, which began in 1961 but was discontinued in 1976, beginning again in 1991 until the present. The trend between 1976 and 1991 is thus unknown.

In addition, CPR estimates of large zooplankton biomass are not considered to be very reliable because large zooplankton (euphausiids) are large compared with the size of the opening to the sampling net (D. Sameoto, Department of Fisheries and Oceans, P.O. Box 1006, Dartmouth, NS B2Y 4A2, Canada, personal communication). With these caveats, the CPR data show that compared with the long-term mean, the abundance of euphausiids was lower in the 1990s than prior to the 1970s (Sameoto 2004). The Ecopath models indicate a twofold increase in large zooplankton biomass from the early 1980s to the late 1990s. These biomass estimates are also considerably higher than estimates taken from the literature. Sameoto and Cochrane (1996) estimated an average biomass of krill of 10 t·km^{-2} in the Emerald and Le Have basins and 2 t·km^{-2} in other areas, based on net and acoustic data.

An estimate of small zooplankton biomass was only available for the late-1990s time period (E. Head and L. Harris, Department of Fisheries and Oceans, P.O. Box 1006, Dartmouth, NS B2Y 4A2, Canada, personal communication; see also appendix 4 in Bundy 2004) and in the absence of other information, this estimate was also used as an input biomass estimate for the early-1980s model. However, the late-1990s balanced model required a greater biomass of small zooplankton than the early-1980s model. Small zooplankton biomass is thus modelled to increase by 29%. CPR data showed a decrease in small zooplankton from the 1960s and early 1970s to the 1990s (Department of Fisheries and Oceans 2003*a*; Sameoto 2004) but again, the missing years of CPR data preclude any firm conclusion as to what occurred between the early 1980s and the late 1990s. The sensitivity analysis indicated that the greatest sensitivity in the model was small zooplankton to large zooplankton. Unfortunately, this is where the data are very poor.

There is also a large degree of uncertainty concerning the input estimates for other lower trophic levels, such as the benthic groups. Essentially, the dynamics of the lower trophic levels are not modelled well, owing to lack of information. Very approximate estimates of biomass were used as input values to these models, and for the benthic groups only 10%–45% of production was used within the model. The question arises as to what happens to the rest of this production. Alternative modelling approaches and better data are required to answer this question. The earlier ecosystem studies by Mills and Fournier (1979) and Mills (1980) did place more focus on the lower trophic levels, including bacteria, meiofauna, and three zooplankton groups, in their hypothetical food webs. However, they noted that data were poor and recommended that detailed studies be carried out before predictive modelling of ecosystems begins. Since then there has been an increase in available data for higher trophic levels, but in some key areas they are still poor. For the models presented here, there was only a reasonable estimate of small zooplankton biomass for one time period.

Biomass accumulation in Ecopath models

The BA term was incorporated into the Ecopath model to move away from steady-state assumptions and allow for changes in biomass over the modelled time period. For some species, such as American plaice, there were clear trends in biomass, and the incorporation of a BA term was straightforward. For other groups it was less clear, and this could have affected model estimates of unknown mortality and biomass. Owing to the constraints of the Ecopath software it was not possible to conduct a sensitivity analysis to the BA terms for all groups in the model, but the effect of including BA terms for sand lance and small pelagics was explored.

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Table 8. Comparison of mortality for sand lance and small pelagics without and with biomass accumulation (BA) terms.

Group	Model type	*Z*	*F*	*M2*	BA	*MO*
Sand lance	No BA	0.62	0.00	0.44	0.00	0.18
	With BA	0.62	0.00	0.44	0.16	0.01
Small pelagics	No BA	0.47	0.09	0.09	0.00	0.38
	With BA	0.47	0.09	0.09	0.10	0.28

Note: All rates are per year. *MO* is "other mortality".

The biomass of forage fish was low in the early 1980s due to cropping by predators, whereas in the late 1990s there were relatively few predators and their biomass was high, resulting in high unknown mortality terms. All of these groups increased during the 1990s, since their predators had been largely removed by fishing, but no BA term was included, owing to the large degree of uncertainty associated with the biomass estimates for these groups. However, a post-hoc BA rate of 0.16 and 0.1·year^{-1} was estimated for sand lance and small pelagics, respectively (based on estimated catchability-adjusted RV-trawl estimates of biomass; see Bundy 2004). If these BA terms are added to the model, the other-mortality term is reduced, especially for sand lance (Table 8). BA indicates that production is much greater than mortality, and that $P/B \neq Z$.

Unfortunately, the BA term is treated as a mortality rate in Ecopath (Christensen et al. 2000), where $P/B = Z$ and Z is the sum of fishing mortality, predation mortality, BA rate, and other mortality. The implication of this is that Ecopath is still embedded in the steady-state assumption. In reality, if mortality is greater (less) than production, biomass will decrease (increase), and a negative (positive) BA term would be used. This would be better expressed as $P/B + \mathrm{BA} = Z$, for this explicitly acknowledges that the steady-state assumption does not hold, and that $P/B \neq Z$. BA should not be treated as a mortality term; it is the consequence of $P/B \neq Z$.

The analysis of the effects of uncertainty in the input data on model estimates was useful and provided some confidence that the widespread increase in trophic level of many groups was significant, and that changes in predation mortality were significant. It also showed that the uncertainty associated with some model estimates was sufficiently wide that it was not possible to detect, with confidence, other differences between the two models, e.g., the network analyses. This type of analysis should be carried out routinely with Ecopath models, although to date, in papers comparing Ecopath models, this step has not been taken (e.g., Christensen 1998; Ortiz and Wolff 2002; Heymans et al. 2004). Unfortunately, there is no easy way to do this, and currently, only biomass and diet can be perturbed with a predefined range of uncertainty. The ranges of uncertainty (in the Pedigree routine) are predefined and limited and the base model value is always in the centre of the distribution. Greater flexibility in the Autobalance routine would enhance this type of analysis. Furthermore, 30 replications is a minimal number of replications with which to do this type of analysis; ideally, there would be close to 10 000 replications. This is currently not possible, owing to the lack of automation in this exercise, but development of a means to do this should be considered as a next step.

There was a considerable temperature change between these two model periods, which may have affected productivity of fish, invertebrates, and plankton. In Ecopath, these changes are reflected in input estimates of biomass, productivity, and consumption. With better estimates, the effects of this temperature change could be better reflected in the models. It could also clarify differences between productivity and mortality and lead to more robust theories concerning changes in abundance.

Mass-balance modelling with Ecopath with Ecosim is only one approach to gaining a wider and greater understanding of the ecosystem and the effects of fishing on its structure and function. Combining it with other modelling approaches that start from different premises should provide a more robust and informative ecosystem analysis. Alternative approaches may support the conclusions drawn here, augment them, or offer alternative views of the ecosystem and its changes. At a very minimum, what has been accomplished here is to put a large set of the known aspects of the ecosystem and its inhabitants into one framework, highlight information gaps, and note where these are important.

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Appendix A

Table A1. Structure of the eastern Scotian Shelf model.

Marine mammals and seabirds	
1. Cetea	Cetaceans
2. Seals	Grey seals (*Halichoerus grypus*)
3. Birds	Seabirds
Fish groups	
4. L.Cod	Large cod (*Gadus morhua*), >40 cm
5. S.Cod	Small cod, ≤40 cm
6. L.Shak	Large silver hake (*Merluccius bilinearis*), >30 cm
7. S.Shak	Small silver hake, ≤30 cm
8. Hadd	Haddock (*Melanogrammus aeglefinus*)
9. A.plaice	American plaice (*Hippoglossoides platessoides*)
10. L.Hal	Large halibut (*Hippoglossus hippoglossus*), >65 cm
11. S.Hal	Small halibut (*Hippoglossus hippoglossus*, *Reinhardtius hippoglossoides*), ≤65 cm
12. Flats	Flounders (Pleuronectidae)
13. Skates	Skates (*Raja* spp.)
14. Dogfish	Dogfish (*Squalus acanthus*)
15. Redfish	Redfish (*Sebastes* spp.)
16. Pollock	Pollock (*Pollachius virens*)
17. T.Mack	Transient mackerel (*Scomber scombrus*)
18. LDPisc	Large demersal piscivores, e.g., white hake (*Urophycis tenuis*), sea raven (*Hemitripterus americanus*), monkfish (*Lophius americanus*), >40 cm
19. SDPisc	Small demersal piscivores, ≤40 cm
20. LDF	Large demersal feeders, e.g., eelpouts (Zoarcidae), wolfish (Anarhichadidae), >30 cm
21. SLDF	Small large demersal feeders, ≤30 cm
22. SDFs	Small demersal feeders (e.g., sculpins (Cottidae), shannies and blennies (Stichaeidae))
23. Cap	Capelin (*Mallotus villotus*)
24. Slance	Sand lance (*Ammodytes dubius*)
25. T.Pels	Transient pelagics, e.g., tunas (*Thunnus* spp.), swordfish (*Xiphias gladius*), sharks)
26. S.Pels	Small pelagics, e.g., Atlantic herring (*Clupea harengus*), Atlantic argentine (*Argentina silus*)
27. Mesop	Small mesopelagics, e.g., lanternfishes (Myctophidae), hatchetfishes (Sternoptychidae)
Invertebrates	
28. Squids	e.g., *Illex illecebrosus*, *Loligo pealeii*
29. LCrab	Large crabs, carapace width (CW) > 50 mm (e.g., snow crab (*Chionoecetes opilio*))
30. SCrab	Small crabs, CW ≤ 50 mm
31. Shrimp	Shrimp (*Pandalus* spp.)
32. Echin	Echinoderms
33. Polyc	Polychaetes
34. Moll	Bivalve molluscs
35. OBI	Other benthic invertebrates
36. LZP	Large zooplankton
37. SZP	Small zooplankton
Primary producers	
38. PHYP	Phytoplankton
Detritus	
39. DET	Detritus

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Table A2. Pedigree ranges describing the percent uncertainty of each of the parameters for the early-1980s and late-1990s models (for example, the range of uncertainty for the biomass of cetaceans is ±50% of the input biomass estimate).

	Early-1980s model					Late-1990s model				
	B	*P/B*	*Q/B*	Diet	Catch	*B*	*P/B*	*Q/B*	Diet	Catch
Cetaceans	50	20	20	60	50	50	20	20	60	50
Grey seals	10	10	10	30	50	10	10	10	30	50
Seabirds	50	70	40	60		50	70	40	60	50
Large cod	10	10	20	50	50	10	10	20	50	50
Small cod	30	40	20	60	50	30	70	10	50	50
Large silver hake	10	10	10	10	50	10	10	10	50	50
Small silver hake	50	40	10	10	50	80	10	10	50	50
Haddock	10	10	20	50	50	10	10	20	10	50
American plaice	10	50	20	50	50	10	50	20	10	50
Large halibut	30	50	80	50	50	30	50	80	50	50
Small halibut	30	60	30	50	50	30	70	10	50	50
Flounders	30	50	80	50	50	30	50	40	10	50
Skates	30	50	80	50	50	30	50	10	50	50
Dogfish	30	50	30	50	50	30	50	20	50	50
Redfish	80	50	30	50	50	50	50	20	50	50
Pollock	30	60	30	50	50	30	20	20	50	50
Transient mackerel	50	40	40	50	50	50	40	40	50	50
Large demersal piscivores	30	50	30	50	50	30	50	40	50	50
Small demersal piscivores	80	70	30	50	50	30	80	40	50	50
Large demersal feeders	80	50	80	50	50	30	50	40	50	50
Small large demersal feeders	80	70	80	50	50	30	80	40	50	50
Small demersal feeders	80	70	80	60	50	30	80	40	50	50
Capelin	30	60	80	80	50	50	80	40	50	50
Sand lance	80	70	80	50	50	50	70	80	50	50
Transient pelagics	50	70	40	50	50	80	70	20	50	50
Small pelagics	80	20	20	50	50	50	20	20	50	50
Small mesopelagics	80	60	60	60	50	80	70	70	60	50
Squids	80	70	20	50	50	80	70	20	60	50
Large crabs	50	50	70	60	50	50	50	70	60	50
Small crabs	80	70	70	60	50	50	70	70	60	50
Shrimp	80	50	80	80	50	80	50	80	70	50
Echinoderms	50	60	60	60	50	50	60	60	60	50
Polychaetes	50	60	60	60	50	50	60	60	60	50
Bivalve molluscs	50	60	60	60	50	50	60	60	60	50
Other benthic invertebrates	50	60	60	60	50	50	60	60	60	50
Large zooplankton	80	20	20	60	50	50	20	20	60	50
Small zooplankton	50	20	80	60	50	30	20	80	60	50
Phytoplankton	50	50				50	50			

Note: See Table A1 for species' scientific names. *B*, biomass; *P/B*, production to biomass ratio; *Q/B*, consumption to biomass ratio.

Appendix B

Table B1 appears on the next page.

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Table B1. Estimates from the early-1980s and late-1990s Ecopath models.

	Early-1980s model					Late-1990s model				
Group	Trophic level	Biomass ($t \cdot km^{-2}$)	*P/B* ($year^{-1}$)	*Q/B* ($year^{-1}$)	EE	Trophic level	Biomass ($t \cdot km^{-2}$)	*P/B* ($year^{-1}$)	*Q/B* ($year^{-1}$)	EE
1. Cetaceans	3.59	0.23	0.04	10.17	*0.00*	3.71	0.26	0.04	10.17	*0.00*
2. Grey seals	4.16	0.03	0.12	11.80	*0.71*	4.36	0.14	0.12	11.80	*0.68*
3. Seabirds	3.27	0.01	0.25	55.00 (77.50)	*0.24*	3.79	0.01	0.25	55.00 (77.50)	*0.24*
4. Large cod	3.68	1.22	0.63	2.10 (1.95)	*0.68*	4.01	0.07	0.50 (1.04)	1.95	*0.12*
5. Small cod	3.36	0.76	0.75 (1.10)	5.02	*0.98*	3.64	0.10	1.40 (2.20)	5.00	*0.97*
6. Large silver hake	3.63	0.80 (1.8)	1.15	7.42	*0.56*	4.10	0.33 (0.49)	0.93	5.51	*0.32*
7. Small silver hake	3.49	2.13 (3.2)	1.02	7.77	*0.95*	3.59	2.23 (3.71)	1.07	5.80	*0.32*
8. Haddock	3.22	0.84	0.45	4.00 (5.19)	*0.89*	3.26	0.50	0.55 (0.51)	4.00 (5.19)	*0.96*
9. American plaice	3.08	1.08	0.25	1.20	*0.57*	3.45	0.60	0.21	1.20	*0.99*
10. Large halibut	4.15	0.05	0.23	1.53	*0.68*	4.30	0.01	0.50	*3.33*	*0.59*
11. Small halibut	3.75	0.02	0.46	2.75	*0.64*	4.01	0.10	0.46	2.75	*0.16*
12. Flounders	3.13	0.65	0.34	2.70	*0.58*	3.28	0.67	0.31	2.70	*0.89*
13. Skates	3.46	0.27	0.2	1.88	*0.66*	3.47	0.10	0.20	1.88	*0.94*
14. Dogfish	3.83	0.24	0.23	2.00 (2.60)	*0.14*	4.05	0.10	0.21	2.00	*0.14*
15. Redfish	3.43	3.40 (5.76)	0.24	2.00 (6.13)	*0.39*	3.44	1.40 (3.44)	0.30 (2.56)	2.00 (6.13)	*0.97*
16. Pollock	3.64	0.98	0.35 (0.31)	3.00 (3.59)	*0.94*	3.80	0.44	0.31	3.00 (3.59)	*0.93*
17. Transient mackerel	3.39	0.6	0.29	2.20	*0.85*	3.38	0.21	0.29	2.20	*0.75*
18. Large demersal piscivores	4.37	0.2	0.3	3.00 (4.22)	*0.55*	4.24	0.05	0.36	3.00 (4.22)	*0.74*
19. Small demersal piscivores	3.95	*0.11* (0.09)	*0.78*	5.20	0.95	3.95	0.08	*0.78*	5.20	*0.47*
20. Large demersal feeders	3.47	*0.10* (0.09)	0.34	*2.29*	0.95	3.50	0.05 (0.04)	0.27	*1.83*	*0.85*
21. Small large demersal feeders	3.27	*0.22* (0.15)	0.70	*4.67*	0.95	3.32	0.12 (0.09)	0.60	*4.00*	*0.94*
22. Small demersal feeders	3.12	*0.26* (0.03)	0.65 (0.50)	4.27	0.95	3.82	0.78 (0.12)	0.65 (0.15)	*4.27*	*0.26*
23. Capelin	3.22	0.03	*0.70*	4.67	*0.92*	3.27	2.90	*1.00*	6.68	*0.64*
24. Sand lance	3.06	1.10 (0.11)	1.15	*7.67*	0.95	3.35	11.20 (22.38)	0.62	4.07	*0.72*
25. Transient pelagics	4.38	0.05 (0.02)	0.24	2.00 (4.00)	*0.39*	4.46	*0.046* (0.01)	0.24	2.00	0.95
26. Small pelagics	3.26	*1.21* (1.15)	0.51	4.59	0.95	3.21	8.50 (17.1)	0.47	4.60	*0.20*
27. Small mesopelagics	3.34	*0.63*	1.40	5.00	0.95	3.35	*0.42*	1.40	5.00	0.95
28. Squids	3.46	*0.66* (0.08)	*0.67*	4.45	0.95	3.48	*0.53* (0.04)	*0.67*	4.45	0.95
29. Large crabs	3.03	0.15	0.16	1.20	*0.51*	3.03	0.31	0.16	1.20	*0.90*
30. Small crabs	2.97	*1.69*	0.30	1.50	0.95	2.97	3.78	0.30	1.50	*0.29*
31. Shrimp	2.45	*2.77* (0.10)	1.70	*11.30*	0.95	2.45	*13.57* (0.20)	1.70	*11.30*	0.95
32. Echinoderms	2.00	63.70	0.60	*6.70*	*0.09*	2.00	63.70	0.60	*6.70*	*0.04*
33. Polychaetes	2.00	11.90	2.00	*27.80*	*0.17*	2.00	11.90	2.00	27.80	*0.46*
34. Bivalve molluscs	2.00	57.40	0.70	*7.78*	*0.02*	2.00	57.40	0.70	7.78	*0.01*
35. Other benthic invertebrates	2.00	4.90	2.50	*12.50*	*0.43*	2.00	4.90	2.50	*12.50*	*0.80*
36. Large zooplankton	2.46	*16.13* (9.00)	3.04	19.50	0.95	2.46	*34.58* (9.00)	3.04	19.50	0.95
37. Small zooplankton	2.00	34.00	8.40	*28.00*	*0.54*	2.00	44.00	8.40	*28.00*	*0.96*
38. Phytoplankton	1.00	34.38	80.73	—	*0.47*	1.00	43.56	52.19	—	*0.76*
39. Detritus	1.00	187.00	—	—	*0.50*	1.00	187.00	—	—	*0.91*

Note: Values in italics are estimated by the models; values in parentheses are the original values adjusted during the balancing process. For species' scientific names see Table A1.

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Can Atlantic cod (*Gadus morhua*) recover? Exploring trophic explanations for the non-recovery of the cod stock on the eastern Scotian Shelf, Canada[1]

Alida Bundy and L. Paul Fanning

Abstract: The Atlantic cod (*Gadus morhua*) stock on the eastern Scotian Shelf collapsed in 1993. Over a decade later, in spite of a fisheries moratorium on cod fishing, this stock is at an all-time low. In parallel with the collapse of the cod stock, the abundance of large cod prey, including forage fish, shrimp, and snow crab, has greatly increased. The key question, which we explore using trophic mass-balance models, is what processes are preventing cod from recovering on the eastern Scotian Shelf? Cod were split into large and small cod. Modelling results indicate high predation pressure on small cod. In addition, small cod compete with the abundant forage fish for decreasing prey, and are in below-average condition. Large cod incur high, but unidentified, mortality that we suggest is derived from the poor condition of small cod carried through to adulthood. As a consequence of the removal of cod by fishing and an ensuing trophic cascade, eastern Scotian Shelf cod are trapped in a vicious circle: their abundance is being kept low by predation, causing an abundance so low that cod cannot compete for prey with their exceptionally abundant competitors. Furthermore, these competitors may also prey on younger stages of cod.

Résumé : Le stock de morues franches (*Gadus morhua*) de la plate-forme néo-écossaise s'est effondré en 1993. Plus d'une décennie plus tard, bien qu'il y ait un moratoire de pêche en vigueur, ce stock a atteint un minimum historique. Parallèlement à l'effondrement de la morue, l'abondance des proies de grande taille de la morue, dont les poissons fourrage, les crevettes et les crabes des neiges, a connu une forte croissance. La question clé est de savoir quels processus empêchent les morues de se rétablir sur la plate-forme néo-écossaise orientale; nous l'abordons à l'aide de modèles de bilans massiques trophiques. Les morues ont été séparées en petites et grandes selon la taille. Les résultats de la modélisation indiquent que la pression de prédation sur les petites morues est importante. De plus, les petites morues doivent faire compétition avec les nombreux poissons fourrage pour obtenir des proies qui se font de plus en plus rares; leur condition physique est aussi inférieure à la moyenne. Les grandes morues subissent une forte mortalité, de nature inconnue, que nous croyons dérivée de la mauvaise condition physique des petites morues qui se maintient jusqu'à l'âge adulte. À cause du retrait des morues par la pêche et de la cascade trophique qui s'ensuit, les morues de la plate-forme néo-écossaise orientale sont prises dans un cercle vicieux : la prédation maintient leur abondance faible, si faible qu'elles n'arrivent pas à faire compétition pour les proies avec leurs compétiteurs qui sont devenus exceptionnellement abondants. De plus, ces compétiteurs font aussi probablement de la prédation sur les jeunes stades de morues.

[Traduit par la Rédaction]

Introduction

Across Maritime Canada, most Atlantic cod (*Gadus morhua*) stocks collapsed in the early 1990s, fisheries moratoria were imposed, and on the eastern Scotian Shelf (Fig. 1) the moratorium is still in place. In the more than 10 years since the closure of the cod fishery on the eastern Scotian Shelf in 1993, there has been no recovery of the cod population; in fact, cod abundance has declined further. The critical question is why has there been no recovery of the cod stock on the eastern Scotian Shelf? This situation is paralleled for offshore northern cod in Newfoundland and Labrador, which have continued to decline despite a moratorium. In other areas where some recovery of biomass had occurred (cod

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A. Bundy.[2] Bedford Institute of Oceanography, Fisheries and Oceans Canada, P.O. Box 1006, Dartmouth, NS B2Y 4A2, Canada.
L.P. Fanning. Food and Agriculture Organization, Subregional Office for the Caribbean, P.O. Box 631-C, Bridgetown, Barbados.

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[2]Corresponding author (e-mail: bundya@mar.dfo-mpo.gc.ca).

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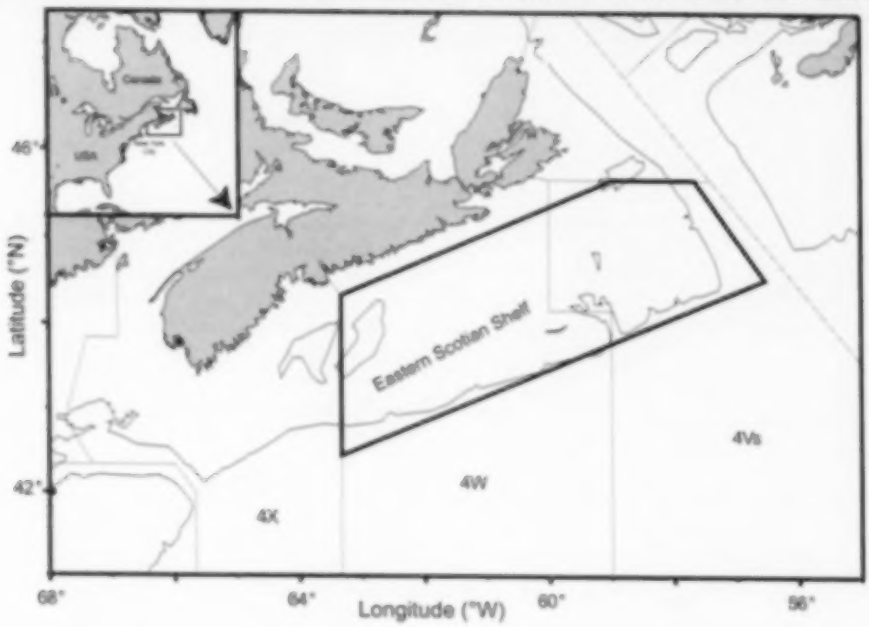
Fig. 1. Map of the Scotian Shelf, showing the eastern Scotian Shelf (NAFO Divisions 4VsW) outlined with a thick line.



stocks in the southern Gulf of St. Lawrence (North Atlantic Fisheries Organization (NAFO) Division 4T); the northern Gulf of St. Lawrence (NAFO Divisions 3Pn4RS); and inshore stocks off Newfoundland and Labrador (NAFO Divisions 2J3KL)), reopening of the fisheries resulted in reclosing or severely restricting them within a few years because of declining biomass (Chouinard et al. 2003; Fréchet et al. 2003; Lilly et al. 2003). So, like the eastern Scotian Shelf stock, these stocks have not recovered. In this paper, trophic explanations for the non-recovery of the cod stock on the eastern Scotian Shelf are explored. It is beyond the scope of this paper to explore similar hypotheses for the other Atlantic cod stocks; however, similar mechanisms may be in evidence.

There are many hypotheses for the non-recovery of cod stocks in Atlantic Canada. Dutil et al. (2003) proposed a low-productivity hypothesis that combines the effects of three factors: low natural intrinsic productivity, a decline in natural intrinsic productivity, and high pressure on production associated with fishing and natural mortality. At a recent meeting of Fisheries and Oceans Canada, over 40 variants of the basic hypotheses were put forward and evidence for many of them was reviewed (Department of Fisheries and Oceans 2003*a*). Those for which there is some basis can be categorized into a few main themes: low productivity and low reproductive potential, high mortality of juvenile and mature cod, even for stocks for which there are no commercial fisheries, poor condition, small size at age and loss of large fish, and loss of spawning components.

Within this range of hypotheses regarding the non-recovery of cod stocks, many evoke a wider ecosystem context to some degree. On the eastern Scotian Shelf, the ecosystem inhabited by cod has changed considerably since the early 1980s. The most obvious changes are in fish species

Fig. 2. Comparison of cod (*Gadus morhua*) biomass (solid line alone) and 5-year average of biomass of forage fish, sand lance (*Ammodytes dubius*), herring (*Clupea harengus*), and capelin (*Mallotus villotus*) (solid line with solid circles).

composition and abundance. Bundy (2005) described the eastern Scotian Shelf as a system that has switched from being dominated by demersal feeders to being dominated by pelagic feeders. With the collapse of the cod stock, there was a concurrent increase in the biomass of forage fish (Fig. 2), including northern sand lance (*Ammodytes dubius*; hereinafter sand lance), Atlantic herring (*Clupea harengus*), and capelin (*Mallotus villotus*). Grey seals (*Halichoerus grypus*), a top predator, and invertebrates such as northern shrimp (*Pandalus borealis*), and snow crab (*Chionoecetes opilio*) have also increased since the late 1980s. Grey seals are considered by some to be an important factor in the mortality of cod. Mortality due to seals is unlikely to have been an important factor in the collapse of cod (Mohn and Bowen 1996). However, in more recent times, even with very low consumption levels, seals could be an important source of

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mortality for the small remaining biomass of cod (Department of Fisheries and Oceans 2003*a*).

In addition to these species changes, the average trophic level of many groups increased, owing to a general increase in piscivory (Bundy 2005). Bundy (2005) hypothesized that piscivory increased because an abundant supply of small forage fish was available. The physical background to these changes in relative species abundance was a marked decrease in bottom temperature on the more easterly part of the eastern Scotian Shelf (Misaine Bank) in the mid-1980s; by the late 1990s, the temperature had risen above normal. These temperature changes demarcate a 15-year period of cold water that is unusual for its intensity and duration. Cold water was also noted along the inshore regions of the eastern Scotian Shelf (Department of Fisheries and Oceans 2003*b*). More detailed reviews of the eastern Scotian Shelf ecosystem are given in Zwanenburg et al. (2002), Zwanenburg (2003), and Department of Fisheries and Oceans (2003*c*).

In this paper, explanations for the non-recovery of cod on the eastern Scotian Shelf are explored in an ecosystem context. The objective of this paper is to explore whether trophic interactions could be a factor in the non-recovery of eastern Scotian Shelf cod by means of Ecopath mass-balance models detailing the trophic links and biomass flows through the eastern Scotian Shelf ecosystem (Bundy 2004, 2005). A comparative approach is taken using mass-balance models for the period before the collapse of the cod, i.e., the early 1980s (1980–1985), and after the collapse, i.e., the late 1990s (1995–2000). The trophic relationships of large and small cod are explored by comparing changes in their mortality rates, their predators, and their prey. A niche-overlap index is used to explore the degree of dietary overlap between large and small cod and other predators and the potential for competition for prey.

Methods

Ecopath (Polovina 1984; Christensen et al. 2000) is a simplified approach to ecosystem modelling that provides a "snapshot" of the ecosystem. It encapsulates the whole biological system, from detritus to top predators, with species aggregated into functional groups to make the model tractable. Trophic interactions are represented through biomass pools, trophically linked through the diet matrix. At its simplest, Ecopath is a bookkeeping tool; at its best, it enables exploration of ecosystem structure and function and analysis of key questions such as the cod non-recovery conundrum.

The key principle of Ecopath is mass balance: for each group represented in the model, the energy removed from that group, for example by predation or fishing, must be balanced by the energy consumed, i.e., consumption. Two linear equations represent the energy balance within a group and the energy balance among groups. Seven data inputs are required: biomass, production or the production to biomass ratio (P/B), consumption or the consumption to biomass ratio (Q/B), and ecotrophic efficiency (EE), in addition to biomass accumulation (BA) (if any), catch, and diet. For primary producers, biomass and production or P/B are required (for further details, see Appendix A). The energy currency used is wet weight, measured in tonnes per square kilometre.

Once the model is balanced, Ecopath estimates a range of indices for ecosystem analysis (Christensen et al. 2000). Several are discussed in Bundy (2005); for further information see Appendix A.

Model parameterization

Where possible, parameter estimates were taken from the eastern Scotian Shelf for the specific time period of the model. When these data were unavailable, data from similar systems and similar time periods were used. Overall, 46% of the data used in the early-1980s model originated from the eastern Scotian Shelf, 49% from similar systems for the same time period, and 35% from the eastern Scotian Shelf for the early 1980s. Of the data used in the late-1990s model, 56% originated from the eastern Scotian Shelf, 54% from similar systems for the same time period, and 54% from the eastern Scotian Shelf for the late 1990s. The effects of changes in environmental conditions on biomass, productivity, consumption, or diet are included in the models, to the extent that they influence these input parameters. The methods and data for the input parameter estimates for each group are given in detail in Bundy (2004), and the general approach is outlined in Bundy (2005). The input parameters for cod are given below and the overall structure of the Ecopath models is provided in Table 1.

Atlantic cod

Atlantic cod were split into two groups to allow for the effects of trophic ontogeny. This split was determined to be at 40 cm, based on the length at capture in the commercial fishery, the length at 50% maturity, and the switch from a mainly invertebrate to a mainly vertebrate diet. In the commercial fishery, while some cod are caught at ages 2 and 3, age 4 is the main recruiting age to the fishery, when they are 43–45 cm in length (Mohn et al. 1998). Age and length at 50% maturity have declined through time from around 4 years and 40 cm in the early 1980s to around 3 years and 34 cm in the late 1990s, respectively (Fanning et al. 2003). Based on cod diet information collected on the eastern Scotian Shelf from 1999 to 2002, the length at which cod switch from a mainly invertebrate to a mainly vertebrate diet is around 40 cm.

The same data sources were used for each time period, unless noted differently. Catch data were taken from Fisheries and Oceans Canada (DFO) catch statistics. For small cod, an estimate of discards during the early 1980s from Fu et al. (2001) was included in the estimate of catch. Biomass was estimated from catchability-corrected estimates from the DFO research vessel (RV) survey and P/B for large cod was estimated from total mortality (R. Mohn, DFO, P.O. Box 1006, Dartmouth, NS B2Y 4A2, Canada, unpublished data), whereas P/B for small cod was estimated from a sequential population analysis. Consumption by large and small cod was estimated from stomach-content data collected during DFO RV surveys of the eastern Scotian Shelf during 1999 and 2000 (Laurinolli et al. 2004). Consumption was then expressed as Q/B by dividing population consumption by population biomass. In the absence of consumption estimates for cod from the eastern Scotian Shelf for the early 1980s, these data were used for both time periods. The input parameter

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Table 1. Structure of the eastern Scotian Shelf model.

Short name	Details
Marine mammals and seabirds	
1. Cetea	Cetaceans
2. Seals	Grey seals (*Halichoerus grypus*)
3. Birds	Seabirds
Fish groups	
4. L.Cod	Large cod (*Gadus morhua*), >40 cm
5. S.Cod	Small cod, ≤40 cm
6. L.Shak	Large silver hake (*Merluccius bilinearis*), >30 cm
7. S.Shak	Small silver hake, ≤30 cm
8. Hadd	Haddock (*Melanogrammus aeglefinus*)
9. A.plaice	American plaice (*Hippoglossoides platessoides*)
10. L.Hal	Large halibut (*Hippoglossus hippoglossus*), >65 cm
11. S.Hal	Small halibut (*H. hippoglossus*, *Reinhardtius hippoglossoides*), ≤65 cm
12. Flats	Flounders (Pleuronectidae)
13. Skates	Skates (*Raja* spp.)
14. Dogfish	Dogfish (*Squalus acanthus*)
15. Redfish	Redfish (*Sebastes* spp.)
16. Pollock	Pollock (*Pollachius virens*)
17. T.Mack	Transient mackerel (*Scomber scombrus*)
18. LDPisc	Large demersal piscivores, e.g., white hake (*Urophycis tenuis*), sea raven (*Hemitripterus americanus*), monkfish (*Lophius americanus*), >40 cm
19. SDPisc	Small demersal piscivores, ≤40 cm
20. LDF	Large demersal feeders, e.g., eelpouts (Zoarcidae), wolfish (Anarhichadidae), >30 cm
21. SLDF	Small large demersal feeders, ≤30 cm
22. SDFs	Small demersal feeders, e.g., sculpins (Cottidae), shannies and blennies (Stichaeidae)
23. Cap	Capelin (*Mallotus villotus*)
24. Slance	Sand lance (*Ammodytes dubius*)
25. T.Pels	Transient pelagics, e.g., tunas (*Thunnus* spp.), swordfish (*Xiphias gladus*), sharks
26. S.Pels	Small pelagics, e.g., herring (*Clupea harengus*), Atlantic argentine (*Argentina silus*)
27. Mesop	Small mesopelagics, e.g., lanternfishes (Myctophidae), hatchetfishes (Sternoptychidae)
Invertebrates	
28. Squids	e.g., short-fin squid (*Illex illecebrosus*), long-fin squid (*Loligo pealeii*)
29. LCrab	Large crabs carapace width (CW) > 50 mm, e.g., snow crab (*Chionoecetes opilio*)
30. SCrab	Small crabs, CW ≤ 50 mm
31. Shrimp	Shrimp, e.g., *Pandalus* spp.
32. Echin	Echinoderms
33. Polyc	Polychaetes
34. Moll	Bivalve molluscs
35. OBI	Other benthic invertebrates
36. LZP	Large zooplankton
37. SZP	Small zooplankton
Primary producers	
38. PHYP	Phytoplankton
Detritus	
39. DET	Detritus

estimates and the final values used in the balanced model are provided (Table 2).

Large and small cod diets for the late-1990s time period were estimated from stomach-content samples taken during the spring and summer RV surveys in 1999 and 2000, with a sample size of 144 for large cod and 345 for small cod (for further details see Bundy 2004). In the absence of cod diet data from the eastern Scotian Shelf for the early 1980s, the diets of large and small cod were estimated using several data sources: data from the western Scotian Shelf for the 1980s (J. Link, National Marine Fisheries Service, 166 Water Street, Woods Hole, MA 02543, USA, personal communication) and DFO diet data from the eastern Scotian Shelf from the 1960s and from 1999 and 2000 (Appendix B, Tables B1 and B2). The diets from 1999 and 2000 were included in the estimation to ensure reasonable consistency between the diets from the eastern Scotian Shelf for the 1960s and the western Scotian Shelf for the 1980s. Although

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Table 2. Ecopath input parameters for large and small cod.

	Input parameter estimates		Balanced model values	
	Early 1980s	Late 1990s	Early 1980s	Late 1990s
Large cod				
Catch (t)	51 974	274	51 974	274
Biomass	124 651	7506	124 651	7506
P/B year^{-1}	0.63	1.04	0.63	0.50
Q/B year^{-1}	1.95	1.95	2.1	1.95
Small cod				
Catch	29 111	0	29 111	0
Biomass	773 222	9732	773 222	9732
P/B year^{-1}	1.1	2.2	0.75	1.4
Q/B year^{-1}	5.0	5.0	5.0	5.0

there are differences between the three diets, there is also reasonable consistency in terms of both presence/absence of prey items and the relative proportions of prey. These 1999–2000 diet data were given little weight in the final estimation of the early-1980s diet for large and small cod.

Uncertainty

To explore the effects of using data from other ecosystems or time periods on model results, a method was developed to explore the effects of uncertainty in Ecopath models (Bundy 2004). A perturbation analysis was carried out once the Ecopath models were balanced, using the Autobalance routine (Kavanagh et al. 2004) and the Pedigree routine in Ecopath. The Autobalance routine randomly selects the initial input parameters from a predefined range of values using the Pedigree routine (see below). Thus, each run starts with a different set of conditions, and the routine searches for the combination of parameters that will produce a balanced model. A balanced model is defined as one where all groups have a EE of less than 1. In this case, the target EE was set to be 0.95. The Autobalance routine was programmed to run for 10 000 runs in order to reach this target.

Only the biomass and diet parameters can be directly perturbed in the Autobalance routine, thus it is not a full perturbation analysis. However, the Autobalance routine does allow P/B and Q/B to be "nudged" from their initial values during the run by predefined steps, to balance the model. In this case, P/B and Q/B were nudged in 10% steps. In practice, in some model balances P/B and Q/B were nudged and in others they were not, depending on the start conditions.

In the Pedigree routine, ranges of percent uncertainty are assigned to the biomass, P/B, Q/B, catch, and diet input or model estimates, based on the origin of the data (e.g., empirical data from the model area, empirical data from a similar area, data from the literature, and Ecopath estimates, which are given a high range of uncertainty). With this routine, the overall Pedigree of the model, which can be compared with that of other models, represents how well the model is grounded in relevant empirical data (see Christensen et al. 2000). The available Pedigree ranges are preset in Ecopath and values range between 10% and 80%, depending on the quality of the data. While this is not a true empirical estimate of the uncertainty associated with the data, it is a step towards exploring the effects of uncertainty on model estimates. The Pedigree ranges were assigned to the two models using both the Ecopath criteria and the author's knowledge of the data (Appendix A, Table A2).

Thirty model runs were completed using the Autobalance routine, providing estimates of 95% confidence limits for all input and output parameters. This is especially useful for exploring the range of feasible solutions for groups with poor parameter estimates, e.g., seabird or shrimp biomass. When comparing the two models, a Mann–Whitney U two independent samples test was used to test whether differences between the models were significant, or an artefact created by the uncertainty of the input parameters. A visual analysis using box-and-whisker plots was used to check whether differences detected by the Mann–Whitney test made sense ecologically. This, together with Bundy (2005), constitutes the first uncertainty analysis of this type with an Ecopath model. It is preliminary, consisting of only 30 replicates, but does provide some rigour for this type of comparative analysis.

Results

High mortality and the non-recovery of cod on the eastern Scotian Shelf

The total mortality of large cod is estimated to have decreased from the early 1980s to the late 1990s, whereas the total mortality of small cod almost doubled (Fig. 3). Fishing mortality of large cod was high in the early 1980s, accounting for 66% of the total mortality. Since the groundfish moratorium was implemented in 1993, it has decreased practically to zero. Other mortality increased in the model, to account for 88% of the total mortality in the late 1990s. Predation mortality was low in both time periods, but increased slightly.

Fishing mortality of small cod was also high in the early 1980s, mostly because of discarding (Fu et al. 2001; Bundy 2004), but decreased to near zero by the late 1990s. In both time periods, predation is estimated to have been the main cause of mortality, increasing from 60% of total mortality in the early 1980s to 97% in the late 1990s.

Predation on large cod

According to the model, predation accounted for only 2%–5% of the total mortality of large cod. They have few identified predators, which were the same in both time periods,

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Fig. 3. Total mortality of large and small cod on the eastern Scotian Shelf in the early 1980s and late 1990s (solid bars denote "other mortality", shaded bars denote predation mortality, and open bars denote fishing mortality).

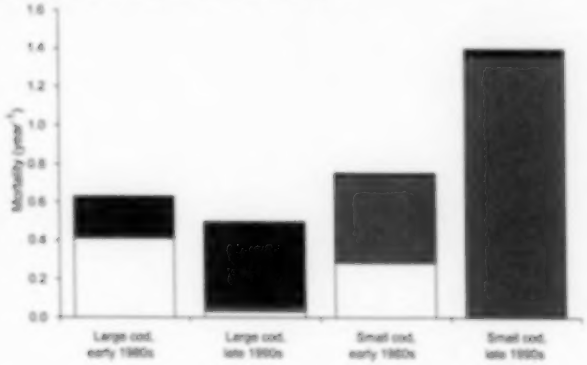
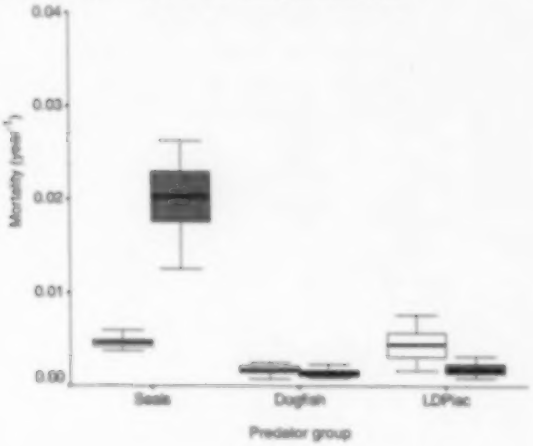


Fig. 4. Box-and-whisker plot comparing predation mortality of large cod on the eastern Scotian Shelf in the early 1980s (open boxes) and late 1990s (shaded boxes) ("LDPisc" is large demersal piscivores). The thick lines represent the median, the boxes represent 50% of the values, and the whiskers extend to the highest and lowest values (excluding outliers, which are cases with values between 1.5 and 3 box lengths from the upper or lower edge of the box; the box length is the interquartile range).



i.e., grey seals, dogfish (*Squalus acanthus*), and demersal piscivores (an aggregate group consisting of white hake (*Urophycis tenuis*), sea raven (*Hemitripterus americanus*), monkfish (*Lophius americanus*), and cusk (*Brosme brosme*); Fig. 4). Predation mortality caused by grey seals is estimated to have significantly increased from the early 1980s to the late 1990s ($U = 0$, $p \leq 0.001$), a change paralleled by an increase in grey seal biomass. The biomass and the mortality caused by the other predators significantly decreased (dogfish: $U = 275$, $p = 0.051$; large demersal piscivores: $U = 52$, $p = 0.001$).

Predation on small cod

The high predation mortality of small cod was caused by a wide range of predators that was consistent across the two time periods (Fig. 5*a*). In both time periods, grey seals and small demersal piscivores were estimated to be the most important predators. Although there is a lot of uncertainty associated with the estimates of predation mortality, all the changes in mortality over the two time periods were significant (large demersal piscivores: $U = 324$, $p = 0.05$; others: $p = 0.001$), with the exception of the mortality caused by dogfish. Total predation mortality of small cod increased by a factor of 3, yet the biomass of most of the predators decreased from the early 1980s to the late 1990s (Fig. 5*b*), with the exception of grey seals, which account for 19% of the predation mortality. Therefore, model results suggest that the high predation mortality does not reflect an increase in predation but a much-reduced biomass.

What do cod feed on and do they have enough?

Large cod are omnivorous and prey on 26 of the other Ecopath groups. The importance of various prey items in the diet has changed between the time periods (Fig. 6*a*). In the early 1980s, 10 prey groups provided 85% of large cod's annual consumption, whereas in the late 1990s this number was reduced to 6: shrimp, sand lance, small pelagics, American plaice (*Hippoglossoides platessoides*), small cod, and large zooplankton. The changes in consumption between the two time periods are significant, with the exception of small halibut (*Hippoglossus hippoglossus*) and large crabs. In particular, the consumption of large zooplankton decreased ($U = 0$, $p = 0.001$), while consumption of shrimp ($U = 0$, $p = 0.001$), small pelagic feeders ($U = 0$, $p = 0.001$), and small cod ($U = 0$, $p = 0.001$) significantly increased. Sand lance was important in the diet of large cod in both time periods, but more so in the late 1990s.

Small cod are also fairly omnivorous, feeding on 21 of the other Ecopath groups, including some cannibalism (Fig. 6*b*). In both time periods, four prey groups made up 85% of annual consumption: in the early 1980s the top four were large zooplankton, other benthic invertebrates, shrimp, and polychaetes; in the late 1990s they were large zooplankton, shrimp, sand lance, and other benthic invertebrates. Consumption of large zooplankton ($U = 280$, $p = 0.05$), other benthic invertebrates ($U = 40$, $p = 0.001$), and polychaetes ($U = 263$, $p = 0.05$) significantly decreased, although there is a high degree of overlap in the distribution of the estimates for large zooplankton and polychaetes (Fig. 6*b*), indicating that these two results are less robust. Consumption of shrimp ($U = 2$, $p = 0.001$), sand lance ($U = 0$, $p = 0.001$), and small pelagic feeders ($U = 0$, $p = 0.001$) significantly increased. Consumption of small and large demersal feeders, squids, American plaice, and small demersal piscivores did not change statistically. There is greater similarity in the diets of small cod across the two time periods than in the diets of large cod.

Adverse changes in prey availability could lead to food limitation for cod. However, the biomass of the three main prey species of large cod in the late 1990s, sand lance ($U = 0$, $p = 0.001$), shrimp ($U = 0$, $p = 0.001$), and small pelagic feeders ($U = 0$, $p = 0.001$) significantly increased from the early 1980s to the late 1990s (Fig. 7), indicating that large cod were unlikely to be food-limited, especially given the low biomass of cod. These prey groups are also important in

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Fig. 5. Box-and-whisker plot comparing (*a*) predation mortality of small cod and (*b*) biomass of predators of small cod on the eastern Scotian Shelf (see Table 1 for an explanation of group names). The thick lines represent the median, the boxes represent 50% of the values (open boxes, the early 1980s; shaded boxes, the late 1990s), and the whiskers extend to the highest and lowest values (excluding outliers, which are cases with values between 1.5 and 3 box lengths from the upper or lower edge of the box; the box length is the interquartile range).

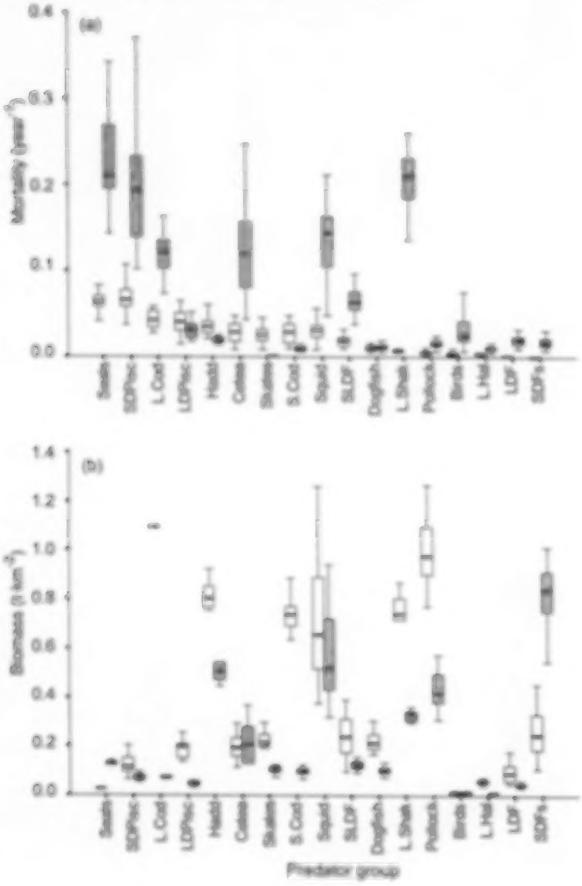
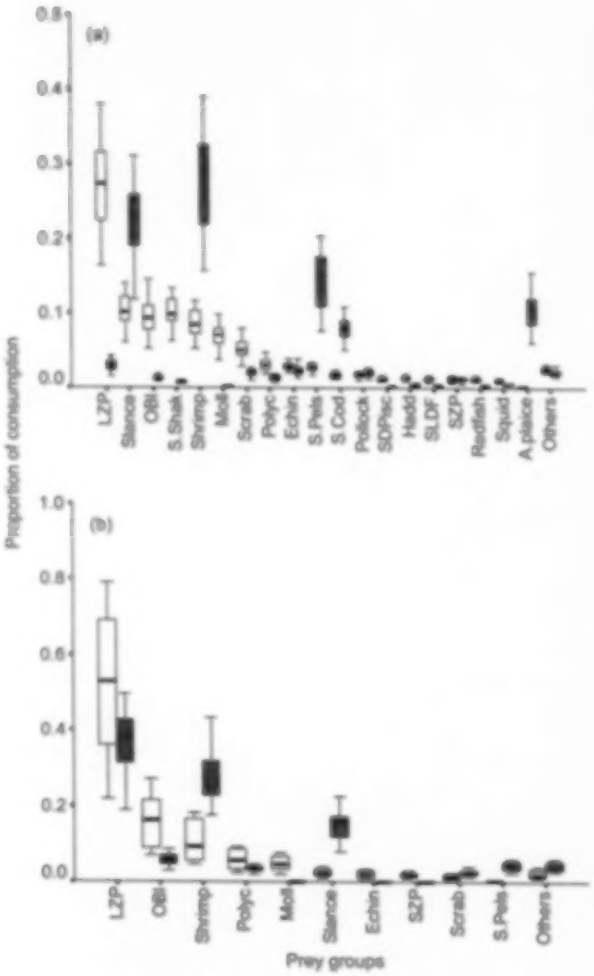


Fig. 6. Box-and-whisker plot comparing proportional diets of (*a*) large cod and (*b*) small cod (see Table 1 for an explanation of group names). The thick lines represent the median, the boxes represent 50% of the values (open boxes, the early 1980s; shaded boxes, the late 1990s), and the whiskers extend to the highest and lowest values (excluding outliers, which are cases with values between 1.5 and 3 box lengths from the upper or lower edge of the box; the box length is the interquartile range).



the diet of small cod. However, the biomass of large zooplankton, the most important prey of small cod in both time periods, is estimated by Ecopath. The estimate increased from the early 1980s to the late 1990s because consumption demands increased, owing to the increase in the biomass of predators of large zooplankton (e.g., sand lance, small pelagic feeders, and shrimp). However, there is a high degree of uncertainty associated with the estimate of large zooplankton biomass and it is not well supported by available data.

Competition for food

Although there may be an abundance of prey, there may also be competition for those prey. This was explored using the niche-overlap index (Appendix A, eq. A4; Christensen and Pauly 1992) for large and small cod. The niche-overlap index indicates the degree of overlap in the diets of various Ecopath groups. Where prey are limited, this may result in competition for resources, assuming that competitors and prey co-occur, spatially and temporally. The average niche overlap between large cod and all their potential competitors was 0.37, and for small cod 0.57, indicating that small cod face more potential competition for resources than large cod do (Table 3). The average niche overlap across all Ecopath groups was 0.38, therefore small cod appear to face a higher than average level of potential competition for resources. Small cod also have the highest niche overlap of all groups.

Large cod have a niche overlap of 0.5 or greater with 12 other Ecopath groups, mostly other piscivorous or gadoid

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Fig. 7. Box-and-whisker plot comparing the biomass of the main prey of large cod on the eastern Scotian Shelf ("Slance" is sand lance and "S.Pels" is small pelagic feeders). The thick lines represent the median, the boxes represent 50% of the values (open boxes, the early 1980s; shaded boxes, the late 1990s), and the whiskers extend to the highest and lowest values (excluding outliers, which are cases with values between 1.5 and 3 box lengths from the upper or lower edge of the box; the box length is the interquartile range).

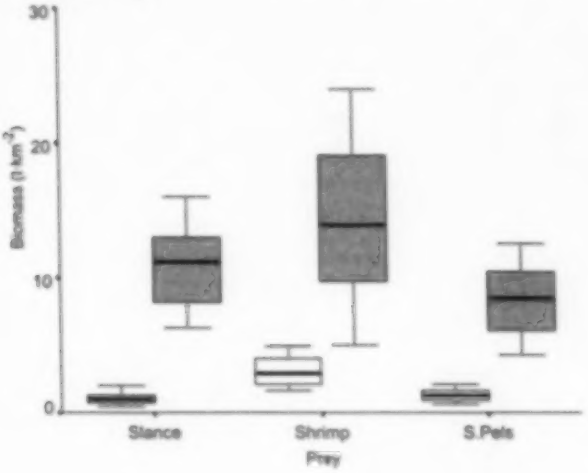

Table 3. Niche-overlap indices for large and small cod in the late 1990s.

Large cod		Small cod	
Ecopath group	Niche-overlap index	Ecopath group	Niche-overlap index
SDPisc	0.81	S.Shak	0.86
L.Hal	0.79	Pollock	0.85
S.Hal	0.68	A.plaice	0.84
S.Cod	0.68	Redfish	0.83
LDF	0.65	Skates	0.83
S.Shak	0.65	SDFs	0.80
LDPisc	0.61	Birds	0.78
Redfish	0.58	SLDF	0.75
SDFs	0.54	Cetea	0.73
Dogfish	0.54	LDF	0.72
A.plaice	0.53	Slance	0.72
Seals	0.50	S.Hal	0.72
		Cap	0.70
		SDPisc	0.70
		L.Cod	0.68
		T.Mack.	0.61
		Squid	0.59
		Flats	0.58
		L.Shak	0.53
		S.Pels	0.52

Note: A niche-overlap index close to zero means little overlap, whereas an index close to 1 means a large overlap. Only indices greater than 0.5 are shown. See Table 1 for Ecopath group names.

fish, e.g., halibut, demersal piscivores, large demersal feeders, small silver hake (*Merluccius bilinearis*), and small cod, but also with redfish (*Sebastes* spp.), dogfish, and grey seals. With the exception of grey seals, small halibuts, small demersal feeders, and small silver hake, the biomass of these groups was lower in the late 1990s than in the early 1980s. In the late 1990s, small silver hake fed heavily on shrimp, the top prey in the diet of large cod. Grey seals, small demersal feeders, and small silver hake are large consumers of sand lance, the second most important prey in the diet of large cod. However, both shrimp and sand lance are very abundant, and indeed there may be surplus production of sand lance in the ecosystem, since the EE of these groups is less than 0.95. Thus, there is unlikely to be competition for these prey.

Twenty Ecopath groups have a niche overlap with small cod that is greater than 0.5. The biomass of several of these — small demersal feeders, sand lance, capelin, and small pelagic feeders — has increased greatly since the early 1980s (Fig. 2), and since they co-occur with cod, they may have increased the competition for resources. The extent of this putative competition was explored by comparing the average annual consumption of various prey by small cod and these competitors. In the early 1980s, consumption by the two groups was comparable (Fig. 8*a*). For example, small cod consumed a similar amount of large zooplankton to sand lance or small pelagic feeders, and a similar amount of other benthic invertebrates to small demersal feeders, sand lance, and small pelagic feeders. However, in the late 1990s, small cod faced stronger competition for resources, particularly for their main prey, large zooplankton (Fig. 8*b*). The average annual consumption of large zooplankton by small cod was 16 000 t, while the estimated total consumption of large zooplankton by sand lance, small pelagic feeders, capelin, and small demersal feeders was 6 million t. Total consumption of large zooplankton by all predators was 10.2 ± 2.8 million t (mean ± SD). Small cod also faced strong competition for their second most important prey item, shrimp. Cod consumed 14 500 t of shrimp annually, while sand lance, capelin, and small pelagic feeders ate an annual total of 1.2 million t. The consumption of shrimp by all predators was 2.2 ± 0.47 million t.

In the Ecopath model, the large zooplankton group is an aggregate that includes euphausiids, amphipods, fish eggs, and fish larvae. Therefore, dietary overlap between small cod and other groups that prey on large zooplankton does not necessarily indicate that they compete for the same species of large zooplankton. To investigate this, the diets of small cod, sand lance, herring (small pelagic feeders), and capelin were explored in more detail using diet data collected from the spring and summer DFO RV surveys from 1996 to 2002 (Laurinolli et al. 2004). These diets were identified to the species level where possible, but broader categories were used for prey that were less common or more difficult to identify. To compare relative consumption by small cod and their predators, the average prey weight per length group was scaled up to the population level, using numbers at length from the DFO RV surveys (Fig. 9).

In spring, the most important large zooplankton in the diet of 68 small cod were fish eggs (78%). However, both herring and sand lance consume far greater amounts of fish eggs than small cod do. In spring, small cod also feed on amphipods and euphausiids, which are also fed on, in far

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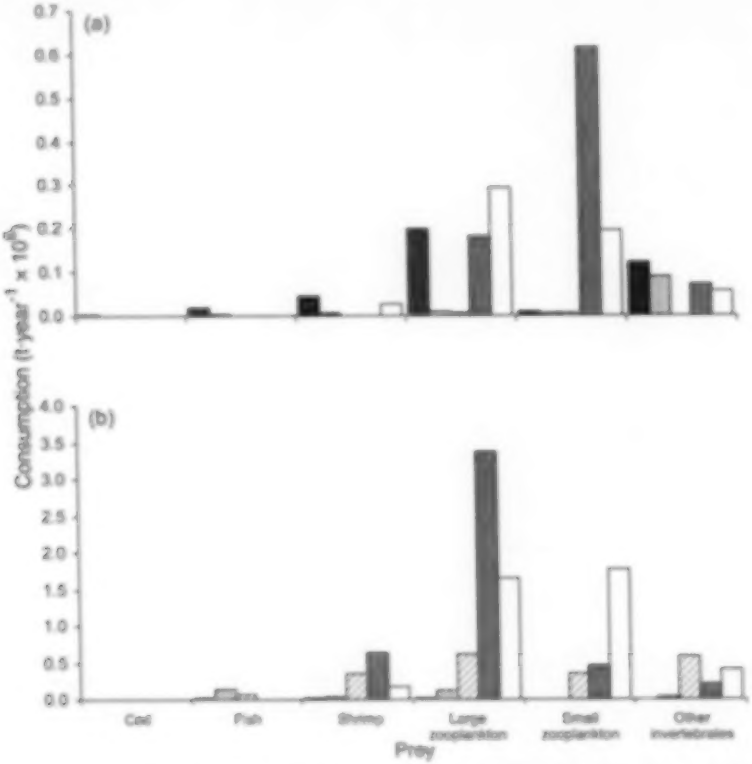
Fig. 8. Comparison of consumption by small cod (solid bars), small demersal feeders (stippled bars), capelin (hatched bars), sand lance (shaded bars), and small pelagic feeders (open bars) of different categories of prey indicated on the *x* axis in (*a*) the early 1980s and (*b*) the late 1990s.



greater amounts, by herring and capelin. In summer the picture was similar: in this case amphipods and euphausiids were both important prey in the large zooplankton diet of small cod (n = 239), but sand lance and small pelagic feeders are much greater consumers of these prey. Thus, in both spring and summer, small cod may compete for large zooplankton with sand lance, herring (small pelagic feeders), and capelin.

Discussion

This analysis of the trophic interactions of Atlantic cod within the eastern Scotian Shelf ecosystem suggests that the lack of recovery of cod stock after its collapse in the early 1990s can be explained by trophic factors, at least for small cod. Small cod may be subject to both high predation pressure and high competition for prey. Large cod have a high unaccounted-for mortality rate and a lower level of potential competition for prey.

The uncertainty analysis adds credibility to these results. It was required to explore the impact on model estimates and comparisons of around 50% of the input data being derived from similar ecosystems rather than from the eastern Scotian Shelf. While this potentially weakens the analysis, the results are generally robust to this uncertainty. Despite the wide ranges of uncertainty used for data from other ecosystems, changes in predation mortality (caused by the main predators) of large and small cod were statistically significant (Mann–Whitney U test). Proxy diets based on similar ecosystems were used for large and small cod for the early-1980s model. While this introduces an undesirable level of uncertainty, significant changes in diets from the early 1980s to the early 1990s, such as increased consumption of shrimp, sand lance, and small pelagic feeders by large cod, make ecological sense in the late-1990s ecosystem.

High mortality and the non-recovery of cod on the eastern Scotian Shelf

The total mortality of large cod has increased since the late 1980s, and estimates now average over 1.0·year^{-1} for the 4+ age group (Fanning et al. 2003). However, this value was reduced to 0.5·year^{-1} in the late-1990s model, owing to thermodynamic constraints. Ecopath uses the steady-state assumption that $P/B = Z$ (Allen 1971). However, for large cod, P/B = 1·year^{-1} created a production/consumption ratio greater than 0.3 and a production/respiration ratio greater than 1. Since thermodynamic constraints limit the production/consumption ratio to between 0.05 and 0.3 and the production/respiration ratio to less than 1 (Christensen et al. 2000), one or more of these parameters required adjustment. P/B was reduced, since it was based on the assumption that $P/B = Z$, while respiration is a model estimate and the con-

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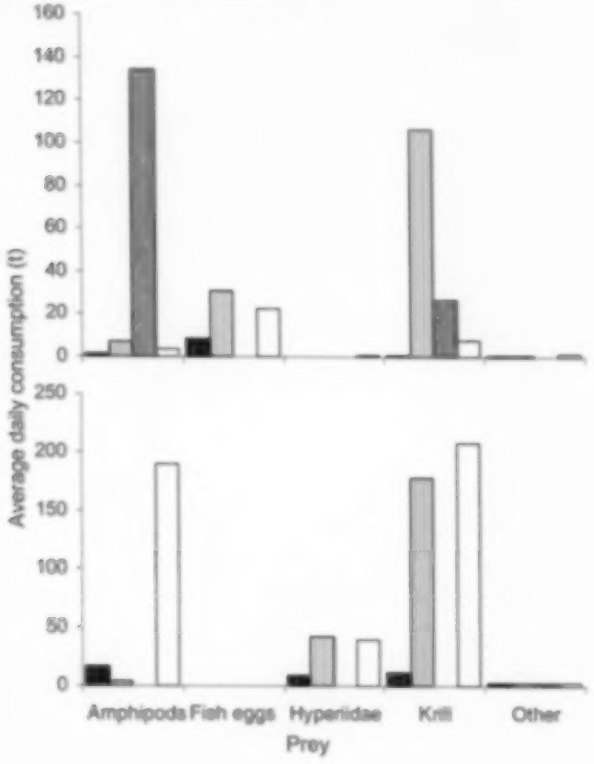
Fig. 9. Average daily prey consumption by the eastern Scotian Shelf populations of small cod (solid bars), herring (stippled bars), capelin (shaded bars), and sand lance (open bars) in (*a*) spring and (*b*) summer (estimated from RV trawl survey data with no adjustment for catchability).



sumption estimate was supported by other studies of cod consumption (Bundy 2004).

The inconsistency between the high estimates of total mortality of large cod from DFO stock assessments, the assumption that $P/B = Z$, and the energetic constraints imposed by the mass-balance Ecopath model requires explanation. Ecopath includes a BA term as a component of mortality (see eq. 2 in Appendix A). However, BA is the consequence of an imbalance between total mortality and P/B and should not be included as part of the mortality term. So if the total mortality of large cod is 1.0·year^{-1} and P/B = 0.5·year^{-1}, there will be a negative BA term of 0.5·year^{-1}. This implies that mortality is greater than production and that until mortality is reduced, production increased, or both, this population will continue to decline. This further supports the hypothesis that the population has fallen into a "predator pit" or some other depensation trap and is now in decline and unable to replace itself.

This raises the issue of the cause of the high "other" mortality of large cod. This other mortality is not due to fishing, since the groundfish fishery on the eastern Scotian Shelf was placed under moratorium in 1993. Cod are caught in the RV and Sentinel surveys and there is a small by-catch of cod in the halibut and redfish fisheries, but total catch form all sources has been less than 300 t since 1998. The implied mortality is only 4% assuming that these catches refer to large cod.

Predation mortality of large cod was low and few predators were identified. Grey seals have been implicated as a source of mortality of cod, especially since the collapse of the cod stock. For grey seals to account for the unknown or "other" mortality of large cod, the proportion of large cod in their diet would have to increase from the estimate of 0.1% used here, to 2%. This is not supported by the latest estimates of grey seals' diet using quantitative assessment of fatty acids. These studies indicate that the total amount of large and small cod in the diet does not exceed an average of 2.6% (S. Iverson, Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada, unpublished data), and since grey seals eat mostly small cod, the proportion of large cod would likely be much less than 2%. Therefore, the most recent data do not support the hypothesis that grey seals are the cause of the high mortality of large cod. The source of high mortality of large cod remains an intriguing question (see below).

On the other hand, small cod are subject to a high predation mortality of 1.36 ± 0.17·year^{-1} (mean ± SD), 97% of their total mortality (1.4 ± 0.08·year^{-1}) or P/B ratio. The high predation rate is not due to an increase in the abundance of the predators of small cod, but to the very low biomass of small cod. This level of predation mortality would be sufficient to prevent the population from increasing even if survival of adult cod was high. Under current circumstances of low rates of adult survival and high rates of predation on small cod, the population will decline.

Are cod losing the competition for large zooplankton?

The low biomass of cod not only makes them vulnerable to predation, but may also increase competition for prey. Small cod compete for their prey with highly abundant competitors, and this likely leads to food limitation. The condition index of both large and small cod has declined since the 1970s and has remained below average since the early 1990s (Fig. 10). Several factors may account for this, including a decrease in water temperature, but for small cod, reduced consumption due to competition for prey is likely to be a contributing factor.

The most important prey of small cod was large zooplankton, particularly euphausiids and amphipods. The Ecopath models indicate a twofold increase in large zooplankton biomass from the early 1980s (16 t·km^{-2}) to the late 1990s (35 t·km^{-2}). These biomass estimates are considerably higher than earlier estimates of euphausiid biomass of 10 t·km^{-2} in the Emerald Basin and 2 t·km^{-2} in the Le Have Basin (Sameoto and Cochrane 1996). However, given that the large zooplankton Ecopath group includes other species in addition to euphausiids, the magnitude of the Ecopath estimates could be correct. Nevertheless, trends in euphausiid and amphipod abundance from the 1960s to the late 1990s (Sameoto 2004) do not support an increase in biomass from the early 1980s to the late 1990s.

There have been no systematic surveys of zooplankton across the Scotian Shelf. The most comprehensive data set is provided by the Continuous Plankton Recorder Survey

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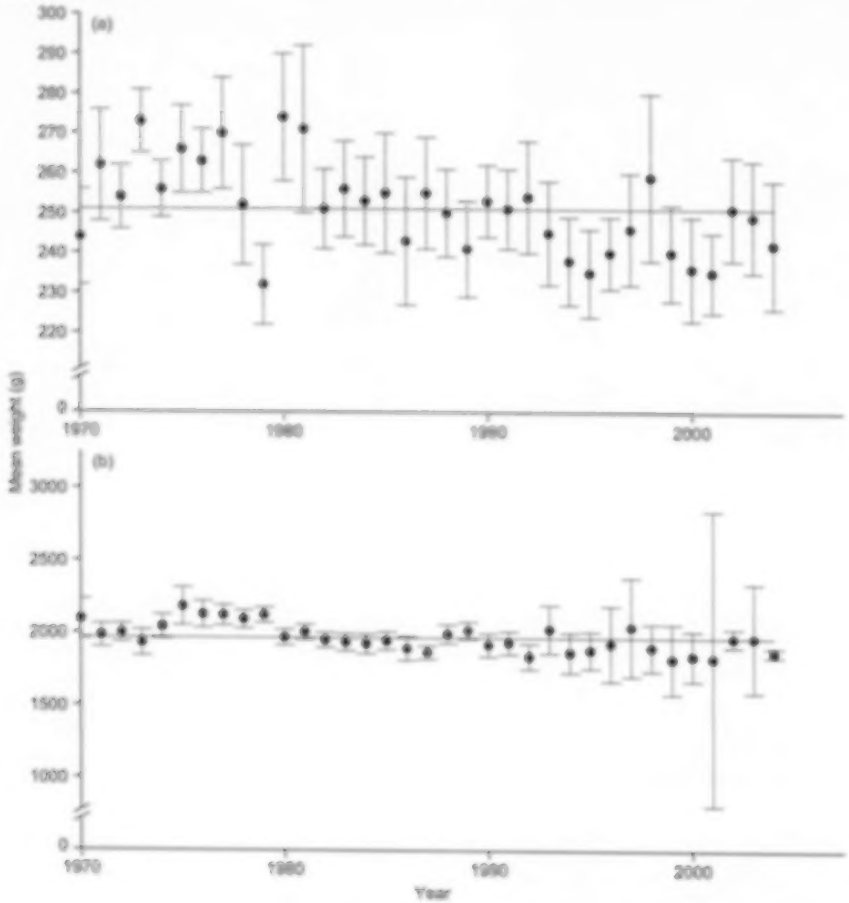
Fig. 10. Condition of (*a*) small (mean weight at 30 cm) and (*b*) large (mean weight at 60 cm) Atlantic cod on the eastern Scotian Shelf. Data points represent the annual mean of the observations, with 95% confidence intervals of the mean. The horizontal line represents the mean over the time series.



(CPR). Data were collected on the Scotian Shelf from 1961 to 1976, then from 1991 until the present. Unfortunately, the missing years include the 1980s, and the trend in abundance between the early 1980s and the late 1990s is unknown. Furthermore, CPR estimates of large zooplankton biomass are not considered very reliable because large zooplankton (euphausiids) are larger than the opening of the sampling net (D. Sameoto, DFO, P.O. Box 1006, Dartmouth, NS B2Y 4A2, Canada, personal communication). With this caveat, the CPR data show that compared with the long-term mean, the abundance of euphausiids was reduced in the 1990s (Sameoto 2004). Therefore, contrary to the Ecopath model results, less large zooplankton biomass was available in the late 1990s than in the early 1980s. The implication of this is that large zooplankton prey were insufficient to meet the consumption demands of their predators, and thus small cod would have experienced increased competition for prey, resulting in reduced per-capita consumption by small cod. This hypothesis is supported by the low condition of small cod during the 1990s.

Beaugrand et al. (2003) reported a similar situation for cod in the North Sea. There, since the late 1980s, the abundance, size, and species diversity of copepods, the food of newly hatched larval cod, have changed, resulting in a reduction of their preferred prey. This change in copepod abundance was associated with a warming of the sea (Beaugrand et al. 2002). Copepods (small zooplankton) may also be important in the diet of young larval cod on the eastern Scotian Shelf. CPR data indicate that copepod abundance on the eastern Scotian Shelf was lower in the early 1990s than in the 1970s (Sameoto 2004). An analysis of data from the Scotian Shelf Ichthyoplankton Survey and the Atlantic Zone Monitoring Program indicates that copepod abundance decreased from the 1980s to the late 1990s (K. Frank, DFO, P.O. Box 1006, Dartmouth, NS B2Y 4A2, Canada, unpublished data). If copepods are important in the diet of larval cod, this could be another contributing factor to the poor condition of cod and their lack of recovery.

This decrease in abundance of euphausiids and copepods was found across the northwest Atlantic Ocean (with the exception of the Gulf of St. Lawrence, which is not included in the CPR) and thus may be a contributory factor to the non-recovery of other cod stocks. Northern cod off the Newfoundland–Labrador banks, for example, are at very low

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biomass, with no predicted recovery at this stage. However, the cod stocks in NAFO Division 3Ps (southwestern Grand Banks) and on the western Scotian Shelf are in better shape, although still much reduced compared with the 1980s.

A changed ecosystem

The main competitors with small cod for large zooplankton and shrimp prey are forage fish: sand lance, small pelagic feeders, and capelin. These three groups increased in abundance at the same time that cod abundance decreased. While the increase in abundance of capelin may be the result of a temporary range extension (Frank et al. 1996), the increase in abundance of sand lance and small pelagic feeders may have been a result of predator release when the cod stocks collapsed. Both were important prey of large cod in the early 1980s.

The cultivation/depensation theory of Walters and Kitchell (2001) proposes that top predators cultivate their young by cropping down forage species that are potential predators and competitors of their young; if top predators are removed (e.g., by fishing), this results in depensatory effects in small cod survival, owing to predation and competition from the now abundant forage species. We suggest that large cod kept the populations of sand lance and small pelagic feeders (herring) in check through predation, and that when large cod collapsed, this enabled the increase in abundance of sand lance and small pelagic feeders, which are now competing with small cod for prey, thereby reducing their survival. Sand lance and small pelagic feeders may also prey on small cod, at either the egg stage or pelagic stage or once they settle on the bottom. There has been no sampling to explore this hypothesis, nor was it possible to explore it with the Ecopath models developed here, since the cod were only split into two large size groups. They would have to be further split into at least one larval group to represent predation on this group

This is reminiscent of a trophic cascade (Carpenter et al. 1985), but is more complex than that described for freshwater lakes. Carpenter et al. (1985) described a single stress point driving the cascade, but here it looks more like a trophic vise. With the exponential increase of seals, cod were squeezed by predation subsequent to being reduced by harvesting, and as the small pelagic feeders increased, this was coupled with competition between small pelagic feeders and young cod, causing the loss of the cultivation effect. At the same time, at least one prey of forage fish, large zooplankton, has decreased with the collapse of the cod stocks and this may be a continuing result of the trophic cascade, where the release of forage fish from top-down control by cod has led to a decrease in large zooplankton prey. Cury et al. (2002) suggest that trophic cascades are seldom seen in open oceans, and that empirical evidence indicates that bottom-up control predominates in marine ecosystems. However, other research suggests that there is evidence for top-down effects in marine ecosystems (e.g., Verity and Smetacek 1996; Bundy 2001; Worm and Myers 2003), and Swain and Sinclair (2000) provided indirect evidence to support the cultivation/depensation hypothesis in the Gulf of St. Lawrence. The changes observed on the eastern Scotian Shelf suggest that top-down effects do operate, at least at higher trophic levels, but that the situation is more complex than simply top down or bottom up.

It is likely that the eastern Scotian Shelf ecosystem is in a new, relatively stable state. The biomass of cod and other groundfish species remains low, the biomass of pelagic fish, shrimp, and snow crab is high, and the abundance of grey seals continues to increase. Low cod biomass makes them vulnerable to depensation, Allee effects (Frank and Brickman 2000), and competition for prey. This biomass has declined further since the early 1990s, while the biomass of their competitors (and possibly predators), sand lance and small pelagic feeders, remains high. Small cod are in poor condition, predation mortality is high, and there is presumably high competition for prey. Furthermore, the abundance of large zooplankton, the most important prey of small cod, may have decreased. Therefore, few small cod survive to age 4; among those that do, there is high mortality. We propose that the high, unexplained mortality of large cod may be a consequence of these adverse factors faced by cod in their early years. Cod are in poor condition when they become large cod, then remain that way. This is supported by the below-average condition of large cod during the 1990s.

For cod abundance to increase, mortality has to decrease and production has to increase. However, we have made the argument that for this to happen, cod abundance has to first increase, i.e., a "Catch 22". Is there any way out of it? The one obvious response to this crisis has already been taken — reduction of mortality through the moratorium on the cod fishery implemented in 1993. It is difficult to see what else can be done other than to reduce the cod catch to zero (there is currently a small by-catch). Ecosystem manipulation is a possibility (e.g., by reducing the abundance of grey seals, forage fish, or both), but the consequences of this type of anthropogenic interference in an already-disturbed and evolving ecosystem are unknown, and there is no guarantee that it would enable a recovery of the cod stock. In fact, if the cultivation hypothesis is correct, removing seals could make things worse. Given the degree of ignorance and the high probability of error, the Law of Unintended Consequences (Merton 1936) suggests that any intervention at this time might well have unintended effects. Ecosystem simulation modelling is ongoing in an attempt to address these types of questions. In the meantime, it may be best to view the collapse and non-recovery of the cod stock as a case study of the above Law in action, brought about not just by error and ignorance but even more by Merton's "imperious immediacy of interest" whereby government and industry wanted the intended results, the harvest of fish, so much that they dismissed the possibility of unintended results. Now, as a consequence, we have an unintended but continuing experiment wherein the conditions under which the eastern Scotian Shelf cod recover, or not, can be further studied.

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Appendix A

The key principle of Ecopath is mass balance: for each group represented in the model, the energy removed from that group, for example by predation or fishing, must be balanced by what goes into it, i.e., consumption. The following

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two equations represent this balanced relationship. The first equation ensures balance between groups in the model:

(A1) $P_i = Y_i + B_i(M2_i + E_i + MO_i + BA_i)$

where, for group i, P_i is annual production, Y_i is annual catch, B_i is annual biomass, $M2_i$ is the total predation rate for group i, E_i is the net migration rate (emigration minus immigration), $MO_i = P_i(1 - EE_i)$ is the "other mortality" rate, EE_i is ecotrophic efficiency, and BA_i is the biomass-accumulation rate.

The second equation, which balances the flows within each group, is

(A2) $Q_i = P_i + R_i + GS_i Q_i$

where, for group i, Q_i is consumption, R_i is respiration, and GS_i is the proportion of food that is not assimilated.

For each secondary consumer group in the model, three of the following four input data are required: biomass, production or the P/B ratio, consumption or the Q/B ratio, and EE, in addition to BA (if any), catch, and diet, which are mandatory. For primary producers, biomass and production or P/B are required.

Once the model is balanced, Ecopath estimates a range of indices for ecosystem analysis. Several of these are discussed in Bundy (2005), and those that are used in this paper are described below.

Total mortality (Z) consists of four components: fishing mortality (F), predation mortality ($M2$), loss (or gain) due to BA, and "other mortality" (MO), which are assumed to be additive. Disease, senescence, and environmental effects can cause other mortality. However, it should also be considered unexplained mortality, or mortality for which the model fails to account. It is assumed in Ecopath that total mortality is equivalent to P/B (Allen 1971), and therefore total mortality is an input value. Ecopath estimates predation, fishing, and "other" mortality.

(A3) $Z = F + M2 + BA + MO$

Predation mortality is estimated as the proportion of the biomass of group i that is consumed by all of its predators, i.e.,

(A4) $$M2_i = \left(\sum_{j=1}^{n} B_j (Q/B)_j \, DC_{ji} \right) / B_i$$

where $M2_i$ is predation mortality of group i, B is the biomass, Q/B_j is the consumption to biomass ratio of predator j, and DC_{ji} is the fraction of prey i in the diet of predator j (Christensen and Pauly 1992).

The niche-overlap index is a simple index of the extent of overlap in prey (or predators) between two groups. It is modified from Pianka's (1973) niche-overlap index and estimated as

(A5) $$O_{jk} = \sum_{i=1}^{n} (p_{ji} \, p_{ki}) / \left(\sum_{i=1}^{n} (p_{ji}^2 + p_{ki}^2) \right) / 2$$

where p_{ji} and p_{ki} are the proportions of the resource i used by groups j and k, respectively. The index is symmetrical and assumes values between 0 and 1. A value of 0 suggests that the two groups do not share resources, 1 indicates complete overlap, and intermediate values show partial overlap in resource utilization (Christensen et al. 2000).

Appendix B

Table B1. Large cod diets 1–5 in 1980–1985.

Prey item	1	2	3	4	5
Small cod	0.004	0.012	0.012	0.012	0.014
Silver hake	0.000	0.000	0.000	0.000	0.000
Small silver hake	0.011	0.132	0.046	0.070	0.080
Haddock	0.003	0.024	0.000	0.009	0.010
American plaice	0.007	0.002	0.011	0.002	0.002
Large halibut	0.000	0.000	0.000	0.000	0.000
Small halibuts	0.000	0.000	0.000	0.001	0.001
Flounders	0.001	0.039	0.006	0.004	0.004
Skates	0.000	0.000	0.000	0.000	0.000
Dogfish	0.000	0.000	0.000	0.000	0.000
Redfish	0.001	0.000	0.014	0.008	0.009
Pollock	0.000	0.012	0.017	0.012	0.014
Transient mackerel	0.000	0.000	0.000	0.000	0.000
Demersal piscivores	0.000	0.003	0.020	0.003	0.003
Demersal piscivores	0.000	0.009	0.000	0.009	0.010
Large demersal feeders	0.000	0.007	0.000	0.007	0.008
Large demersal feeders, <30 cm	0.002	0.062	0.000	0.062	0.070
Small demersal feeders	0.006	0.006	0.029	0.006	0.007
Capelin	0.005	0.000	0.042	0.000	0.000
Sand lance	0.255	0.077	0.129	0.077	0.087
Transient pelagic feeders	0.000	0.000	0.000	0.000	0.000
Small pelagic feeders	0.016	0.141	0.020	0.018	0.020

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Table B1 (*concluded*).

Prey item	1	2	3	4	5
Small mesopelagic feeders	0.001	0.000	0.000	0.000	0.000
Squid	0.011	0.020	0.005	0.008	0.009
Large crabs	0.000	0.001	0.000	0.001	0.001
Small crabs	0.057	0.234	0.212	0.135	0.153
Shrimp	0.097	0.074	0.230	0.074	0.085
Echinoderms	0.026	0.023	0.062	0.023	0.027
Polychaetes	0.028	0.006	0.011	0.028	0.032
Bivalve molluscs	0.128	0.020	0.020	0.020	0.022
Other benthic invertebrates	0.046	0.011	0.022	0.046	0.052
Large zooplankton	0.295	0.036	0.073	0.234	0.266
Small zooplankton	0.001	0.049	0.020	0.010	0.012
Phytoplankton	0.000	0.000	0.000	0.000	0.000
Detritus	0.000	0.000	0.000	0.000	0.000
Totals	1.000	1.000	1.000	0.878	1.000

Note: Diet 1 is the average annual diet derived from DFO pre-1970s data for the eastern Scotian Shelf (Laurinolli et al. 2004); diet 2 is the average annual diet from the western Scotian Shelf, derived from National Marine Fisheries Service surveys (J. Link, National Marine Fisheries Service, 166 Water Street, Woods Hole, MA 02543, USA, personal communication); diet 3 is the average annual diet from the eastern Scotian Shelf for the 1990s, derived from DFO stomach-content sampling in 1999 and 2000; diet 4 is a subjective amalgam of diets 1–3; and diet 5 is diet 4 normalized.

Table B2. Small cod diets 1–4 in 1980–1985.

Prey item	1	2	3	4
Small cod	0.000	0.004	0.004	0.004
Silver hake	0	0	0	0
Small silver hake	0.002	0.000	0.002	0.002
Haddock	0	0	0	0
American plaice	0.000	0.000	0.000	0.000
Halibuts	0	0	0	0
Small halibuts	0	0	0	0
Flounders	0	0	0	0
Skates	0	0	0	0
Dogfish	0	0	0	0
Redfish	0.001	0.000	0.001	0.001
Pollock	0.000	0.002	0.002	0.002
Transient mackerel	0	0	0	0
Demersal piscivores	0	0	0	0
Demersal piscivores	0.000	0.000	0.000	0.000
Large demersal feeders	0	0	0	0
Large demersal feeders, <30 cm	0.001	0.000	0.001	0.001
Small demersal feeders	0.002	0.049	0.002	0.003
Capelin	0.039	0.013	0.000	
Sand lance	0.097	0.165	0.097	0.100
Transient pelagic feeders	0	0	0	0
Small pelagic feeders	0.003	0.022	0.003	0.003
Small mesopelagic feeders	0	0	0	0
Squid	0.001	0.007	0.001	0.001
Large crabs	0	0.001	0.000	0
Small crabs	0.049	0.137	0.049	0.051
Shrimp	0.113	0.308	0.113	0.117
Echinoderms	0.020	0.079	0.020	0.021
Polychaetes	0.057	0.002	0.057	0.059
Bivalve molluscs	0.048	0.028	0.048	0.049
Other benthic invertebrates	0.040	0.042	0.040	0.041
Large zooplankton	0.507	0.134	0.507	0.525
Small zooplankton	0.019	0.000	0.019	0.020

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Table B2 (*concluded*).

Prey item	1	2	3	4
Phytoplankton	0	0	0	0
Detritus	0	0	0	0
Totals	1.000	0.993	0.967	1.000

Note: Diet 1 is the average annual diet derived from DFO pre-1970s data for the eastern Scotian Shelf (Laurinolli et al. 2004); diet 2 is the average annual diet from the eastern Scotian Shelf for the 1990s, derived from DFO stomach-content sampling in 1999; diet 3 is a subjective amalgam of diets 1–3; and diet 4 is diet 3 normalized.

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Multispecies modelling of some components of the marine community of northern and central Patagonia, Argentina[1]

Mariano Koen-Alonso and Peter Yodzis

Abstract: Using a bioenergetic and allometric approach, we developed multispecies trophodynamic models of the marine community of northern and central Patagonia in the southwestern South Atlantic Ocean that included hake (*Merluccius hubbsi*), squid (*Illex argentinus*), anchovy (*Engraulis anchoita*), and South American sea lions (*Otaria flavescens*). We used these to explore the effects of model structure and parameter uncertainty on predictions of the effects of different management regimes using continuation and bifurcation analysis. We considered five different functional responses and used the Akaike Information Criterion for model selection. The best models involved laissez-faire Holling Type III-shaped functional responses and the worst one corresponded to the Ecosim form. These models showed many similar behaviours but also showed marked differences in some exploitation scenarios. This suggests that using a single model structure as the basis for managing these stocks could lead to misleading, and potentially dangerous, conclusions.

Résumé : Une approche bioénergétique et allométrique nous sert à mettre au point des modèles trophodynamiques multispécifiques de la communauté marine du nord et du centre de la Patagonie dans le sud-ouest de l'Atlantique Sud qui regroupe le merlu argentin (*Merluccius hubbsi*), l'encornet rouge argentin (*Illex argentinus*), l'anchois (*Engraulis anchoita*) et le lion de mer austral (*Otaria flavescens*). Les modèles nous permettent d'étudier, à l'aide d'une analyse de continuation-bifurcation, les effets de la structure du modèle et de l'incertitude des paramètres sur les prédictions des effets de différents régimes de gestion. Nous examinons cinq différents types de réponses fonctionnelles et utilisons le critère d'information d'Akaike pour le choix du modèle. Le meilleur modèle contient des réponses fonctionnelles de type « laisser-aller » de forme III de Holling et le pire correspond à la forme Ecosim. Ces modèles possèdent plusieurs comportements similaires, mais ils présentent des différences marquées pour certains scénarios d'exploitation. Cette observation montre que l'utilisation d'une seule structure de modèle comme base de la gestion de ces stocks pourrait mener à des conclusions trompeuses et potentiellement dangereuses.

[Traduit par la Rédaction]

Introduction

The notion that fisheries affect much more than just the species being fished is undoubtedly widespread and accepted worldwide. Ecosystem and multispecies models are being used increasingly often to account for these effects (Hollowed et al. 2000; Whipple et al. 2000; Fulton et al. 2003). However, the popularity of the concept that we are exploiting systems rather than specific species/resources (e.g., the Symposium on Ecosystem Effects of Fishing held by the International Council for the Exploration of the Sea's Scientific Committee on Oceanic Research; Hollingworth 2000), the efforts to define and frame ecosystem-based management (Link 2002*a*, 2002*b*), and the advocacy of holistic approaches to fishery management (Agardy 2003) do not mean that we understand how exploited ecosystems really work. Actually, our understanding of ecosystem functioning is far from accurate or complete. In the last 30 years we have progressed a lot, from both theoretical (e.g., Polis and Winemiller 1996) and applied perspectives (e.g., Sinclair and Valdimarsson 2003), but there is still a long way to go (Link 2002*b*; Fulton et al. 2003; Stefansson 2003). Today, in many

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M. Koen-Alonso.[2] Northwest Atlantic Fisheries Centre, Department of Fisheries and Oceans, 80 East White Hills Road, P.O. Box 5667, St. John's, NL A1C 5X1, Canada.
P. Yodzis.[3] Department of Zoology, University of Guelph, Guelph, ON N1G 2W1, Canada.

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[2]Corresponding author (e-mail: Koen-AlonsoM@dfo-mpo.gc.ca).
[3]Deceased.

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ways, we are still discussing which is the best way of grabbing this bull and where the horns are located.

Another facet of the problem is that in today's marine ecosystems, fisheries are becoming just one of the activities that take place in them and (or) use their resources (Rosenberg 2003), and not necessarily the most important one. Oil and gas exploration and exploitation, transport of goods, aquaculture, and tourism/leisure are some of the activities that also use marine resources and (or) habitats, and hence, the management of marine systems expands from a traditional, typically fishery-oriented one to a more complex and broader one (e.g., Crespo and Hall 2002; Sainsbury and Sumaila 2003). Many of the current management and conservation questions are framed within the context of ecosystems and communities, and only by looking at and addressing them at these levels will we have some hope of success.

Furthermore, while the distribution of many of these problems is global (e.g., Myers and Worm 2003), it is unlikely that the solutions will be. Each exploited system (i.e., ecosystem + human activities) has its own idiosyncratic features that make it unique. Effective solutions will likely need to be locally tailored. However, if there are truly general ecological mechanisms, and we believe that this is so, the ecological processes involved in the regulation and dynamics of these exploited systems are likely to be common to all of them. In each case, taxonomical identities, food-web structures, environmental/climatic forcing, and relative regulatory importance may vary, but the ecological processes involved should remain the same. Therefore, modelling and comparing these exploited ecosystems with mechanistically oriented approaches should help us to understand how they are regulated and how the different processes are integrated. From this perspective, the present study tries to provide some insight into one specific case, with the hope that it can also contribute to elucidating some of the common issues.

The biological community involved in this analysis is the marine community of northern and central Patagonia on the Argentine continental shelf in the southwestern South Atlantic Ocean, coarsely bounded by 41 and 48°S. The core species in this community are the Argentine hake (*Merluccius hubbsi*), the Argentine anchoita or anchovy (*Engraulis anchoita*), and the squid *Illex argentinus* (Angelescu and Prenski 1987). The rest of the food web is built around the tritrophic system constituted by them (Angelescu and Prenski 1987) (Fig. 1). Hake, squid, and anchovy are also the main common prey of a large suite of top predators, including the sea lion *Otaria flavescens* (Koen-Alonso et al. 2000*a*), dolphins (e.g., *Lagenorhynchus obscurus* and *Cephalorhynchus commersonnii*) (Koen-Alonso et al. 1998; Dans et al. 2003), dogfish and sharks (e.g., *Squalus acanthias* and *Galeorhinus galeus*, respectively) (Koen-Alonso et al. 2002; Dans et al. 2003), and the beaked skate (*Dipturus chilensis*) (Koen-Alonso et al. 2001). The hake supports the most traditional commercial fishery in the region since the 1970s, with reported landings around 500 000 t per year in the 1990s. Also in that decade, the hake stock virtually collapsed (Aubone et al. 1999). The squid fishery developed in the 1980s and was as important as the hake fishery in terms of landings during the late 1990s (Brunetti et al. 1999*a*, 1999*b*). The Patagonian anchovy stock is also fished, but with catches of less than 10 000 t per year, which is below the total allowable catch for this stock (Hansen 1999). Another important fishery in this region is the shrimp (*Pleoticus muelleri*) fishery, but its socioeconomic importance is associated with the higher revenues it generates and not with its catch levels (ranging between roughly 10 000 and 30 000 t·year^{-1} during the past decade) (Bertuche et al. 1999).

Among the top predators, the sea lion is the most conspicuous for our purpose here. This species was drastically reduced between 1930 and 1960, and is believed to have dropped from approximately 200 000 individuals to fewer than 18 000 between 1938 and 1946 in northern Patagonia (Crespo and Pedraza 1991; Dans et al. 2004), where the most intense harvesting took place (Reyes et al. 1999; Dans et al. 2004). Even though the central-Patagonia stock suffered a much smaller harvest, it also dropped dramatically, which strongly suggests that the two nominal stocks have a common population identity (Reyes et al. 1999). Signs of population recovery were not detected until 1990 (Crespo and Pedraza 1991), but it is believed that the population has been recovering since the end of the harvest (Reyes et al. 1999; Dans et al. 2004). Although recent estimates of abundance indicate that this population is still below the pre-harvest level (Dans et al. 2004), the sea lion is today the most abundant marine mammal in the region that actually forages on the continental shelf, and hake and squid are among its main prey items (Koen-Alonso et al. 2000*a*). Sea lions are also one of the wildlife attractions that sustain the growing tourism activity in Patagonia (Tagliorete and Losano 1996).

Our purpose here is to develop simple trophodynamic models that integrate the dynamics of squid, anchovy, hake, and sea lion and the corresponding harvesting impacts on these populations, and to evaluate how these models behave under different exploitation scenarios. We do not aim here to develop management models (i.e., accurate enough to support management decisions); rather, we are trying to explore how these species might be interacting, and also how our choice of model structures, together with parameter uncertainty, may influence our conclusions.

Methods

The system modelled

We have a fairly good understanding of the marine food web of northern and central Patagonia (Fig. 1). However, from a time-series perspective, we have very few data to incorporate into that picture. This is the main reason for focussing our modelling attempt on the core species of this community, for which, fortunately, we have a reasonable amount of data (see the next section).

We know that, among the key species, hake feed primarily on anchovy, squid, and zooplankton, although other prey and cannibalism are, to a lesser extent, also part of the picture (Prenski and Angelescu 1993). The anchovy is the most important forage fish in this community and, like the squid, feeds mainly, but not exclusively, on zooplankton (Angelescu 1982; Ivanovic and Brunetti 1994). The sea lion is a generalist and opportunistic predator, but hake and squid are important components of its diet (Koen-Alonso et al.

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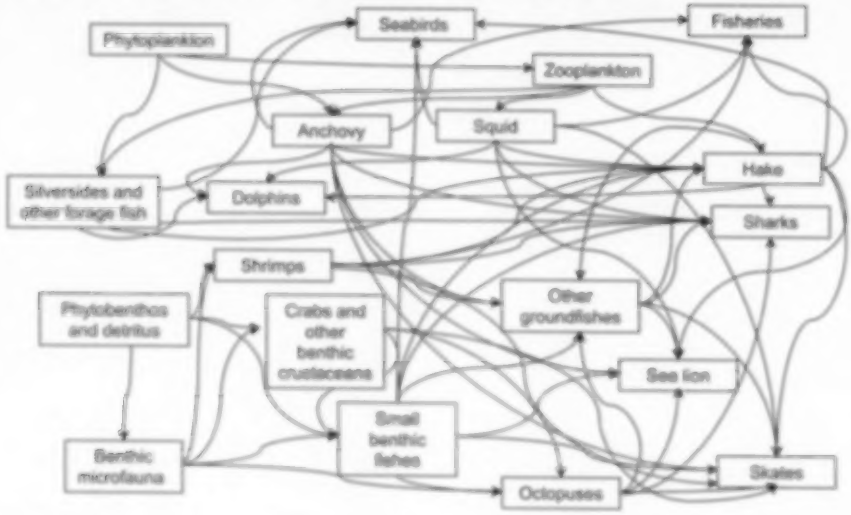
Fig. 1. Simplified food web for the marine community of northern and central Patagonia.



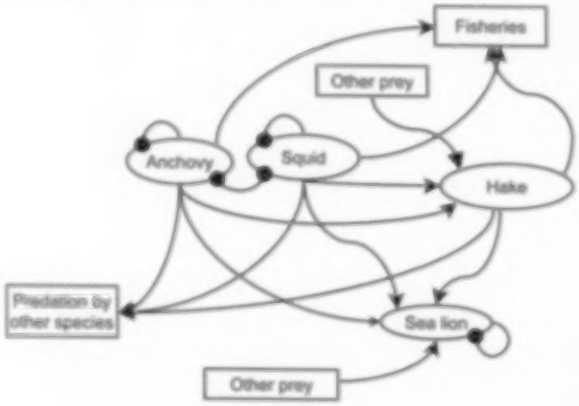
2000*a*). The resulting food web of core species is not a closed system, but incorporates the expected inputs and outputs from and to the rest of the food web as well as outputs to the fisheries (Fig. 2). Because we have no zooplankton abundance data, anchovy and squid are shown without prey. Instead, they are assigned carrying capacities and — to express their dietary overlap — competition coefficients.

In terms of stock identities, the system consists of the summer and south-Patagonian spawning stocks of squid (Brunetti et al. 1999*a*), the Patagonian stocks of anchovy and hake (Aubone et al. 1999; Hansen 1999), and the north- and central-Patagonian population of sea lions (Crespo and Pedraza 1991; Reyes et al. 1999; Dans et al. 2004). There are other stocks of hake, anchovy, and squid on the Argentine continental shelf (Aubone et al. 1999; Brunetti et al. 1999*a*; Hansen 1999), but they are mainly associated with the Bonaerensis region (north of 41°S), and belong to a different species assemblage (Angelescu and Prenski 1987).

The data

The type, quality, and amount of data are always the main constraint in the development of multispecies models. In our case, we had available a heterogeneous database from many different sources that included primary literature, technical reports, theses, and unpublished information. We sorted, organized, and standardized this information to build a single and coherent database that contains estimates of stock biomasses and fishery catches over time periods ranging from 10 to 30 years. For example, sometimes we needed to build the biomass estimates from censuses of individuals and individual mean weights (e.g., sea lion biomass), reconstruct total catches from national and foreign/international catch databases (e.g., for hake and squid), estimate annual catches from previous models (e.g., for sea lions), make decisions about contradictory information (e.g., differences in reported catches among sources), etc. Therefore, each time series represents our best effort to build a coherent overall database with as many data as possible. In this way, even if our data

Fig. 2. General structure of the Patagonian models. The ovals correspond to the dynamic equations for squid (*Illex argentinus*), anchovy (*Engraulis anchoita*), hake (*Merluccius hubbsi*), and sea lion (*Otaria flavescens*) (the first two with basal equations and the other two with consumer equations); the boxes correspond to constant rates (predation by other species) or components ("other prey" is a constant food biomass in the functional responses). The negative self-loop for the sea lion indicates density-dependent mortality, while the negative self-loops for anchovy and squid correspond to the self-limitation imposed by their carrying capacities. The double negative link between anchovy and squid indicates Lotka–Volterra competition.



are not perfect, they represent in a reasonable way the abundances and catches for the populations considered.

The sources consulted were Otero and Simonnazzi (1980), Angelescu (1982), Otero et al. (1982), Angelescu and Prenski (1987), Crespo (1988), Otero and Verazay (1988), Cousseau et al. (1981), Ciechomski and Sánchez (1988), Brunetti and Pérez Comas (1989), Crespo and Pedraza (1991), Programa de Modernización de los Servicios Agropecuarios, Secretaría de Agricultura Ganadería y Pesca and Instituto Inter-

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americano de Cooperación para la Agricultura (1992, 1993, 1994, 1995), Prenski and Angelescu (1993), Bezzi et al. (1994), Santos (1994), Bezzi and Dato (1995), Guía Pesquera Argentina (1995), Bambill et al. (1996), Dans et al. (1996), Hansen and Madirolas (1996), Anonymous (1997), Dato (1997), Pájaro et al. (1997), Brunetti et al. (1998, 1999*a*, 1999*b*), Aubone et al. (1999) Hansen (1999), Reyes et al. (1999), Aubone (2000), Dato et al. (2000), Pérez (2000), and unpublished information from N. Brunetti, National Institute of Fisheries Research and Development of Argentina (INIDEP), Casilla de Correo 175, 7600 Mar del Plata, Buenos Aires, Argentina, E.A. Crespo, Patagonian National Centre (CENPAT; a research centre of the National Research Council of Argentina), Boulevard Brown 3600, 9120 Puerto Madryn, Chubut, Argentina, S. Dans (CENPAT), S. García de la Rosa (INIDEP), M. Lasta (INIDEP), M. Pérez (INIDEP), B. Prenski (formerly of INIDEP), F. Sánchez (INIDEP), and R. Sánchez (INIDEP).

The database (Appendix A) contains biomass estimates for squid (N_s = 10 for the period 1982–1999), anchovy (N_a = 14 for the period 1970–1999), hake (N_h = 30 for the period 1970–1999), and sea lion (N_l = 16 for the period 1972–1998), together with catch estimates for these species. The catch time series for squid, anchovy, and hake covers the period 1970–1999, while the sea lion catches cover the period 1929–1960. Outside these periods we assumed no catches for the modelled stocks. This assumption is not fully realistic but is still reasonable. For example, even though there was a hake fishery before 1970, catches were comparatively small and came mainly from the Bonaerensis region (i.e., they affected a stock not modelled here).

The modelling approach

The models are based on a bioenergetic and allometric framework (Yodzis and Innes 1992; Yodzis 1998). We need to specify two different types of equations: basal and consumer. A basal equation describes the dynamic of a species that does not prey upon others also included in the model. Conversely, a consumer equation represents a species that does prey on others included in the model.

A general expression for the basal equation is

$$(1)\qquad \frac{dB_j}{dt} = \left[r_j \frac{B_j}{K_j}\left(K_j - B_j - \sum_c \alpha_{jc} B_c \right)\right] - \sum_i B_i F_{ji} - m_j B_j - H_j$$

where B_j is the biomass of species j, r_j is its intrinsic production/biomass ratio, K_j is its carrying capacity, α_{jc} is the competition coefficient between species j and a competitor species, c, B_c is the biomass of this competitor (the summation over c indicates a summation over all competitors of species j), F_{ji} is the functional response of predator i when preying on species j, B_i is the biomass of this predator (the summation over i indicates a summation over all predators of species j), m_j is the "other mortality" rate of j and represents losses due to predation by species not included in the model, and H_j is the harvest rate of species j.

Following the bioenergetic and allometric approach (Yodzis and Innes 1992; Yodzis 1998), r_j was modelled as

$$(2)\qquad r_j = f_{r_j} a_{r_j} w_j^{-0.25}$$

where f_{r_j} represents the fraction ($0 < f_{r_j} \leq 1$) of the maximum physiological capacity for production actually realized by species j, a_{r_j} is an allometric coefficient that depends on the metabolic type of species j (endotherm, vertebrate ectotherm, invertebrate, or phytoplankton), and w_j is the mean individual biomass of species j (Yodzis and Innes 1992).

A general expression for the consumer equation is

$$(3)\qquad \frac{dB_j}{dt} = B_j\left(-T_j + \sum_k e_{kj} F_{kj} \right) - \sum_i B_i F_{ji} - m_j B_j - \mu_j B_j^{\nu_j} - H_j$$

where T_j is the mass-specific respiration rate of species j, e_{kj} is the assimilation efficiency of predator j when eating prey k, F_{kj} is the functional response of species j preying on species k (the summation over k indicates a summation over all prey of species j), and the term $\mu_j B_j^{\nu_j}$ represents density-dependent mortality, μ_j being a constant coefficient and ν_j the exponent specifying the density-dependence. The other parameters were already described in the basal equation (for a complete list of the symbols used in this paper see Appendix B).

In similar way to r_j, T_j was modelled as

$$(4)\qquad T_j = a_{T_j} w_j^{-0.25}$$

where a_{T_j} is another allometric coefficient that also depends on the organism's metabolic type (Yodzis and Innes 1992).

The functional response

The functional response is a core structural feature of a trophodynamic model (Yodzis 1994). Its precise mathematical form represents the researcher's view of the biological details of that particular predation process and profoundly affects model behaviour. In most cases, however, so little is known of these biological details that there is only weak evidence, if any, that points towards a given specific mathematical formulation. Under these circumstances, it is essential to avoid the temptation to assume some particular form for the functional response and proceed on that basis to get answers that are reassuringly, but meaninglessly, definitive. Rather, one needs to explore the range of behaviours that are consistent with what we do know about the system.

We therefore fitted the same general model using five different functional responses: multispecies Holling Type II with predator interference (T2), multispecies generalized Holling (GH), frequency-dependent predation (FD), Evans (EV), and Ecosim (EC). Four of these functional responses (T2, GH, FD, and EV) can easily be derived from a more general expression for handling-time/satiation-limited functional responses (i.e., the predator's consumption rate reaches an asymptotic maximum when prey density increases). The fifth one, the Ecosim functional response, was included because of its wide use as part of the Ecopath with Ecosim software package (Walters et al. 1997; Walters and Kitchell 2001).

If we derive the functional response from time budgeting and simple foraging theory we can write a fairly general

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form for many functional responses (eq. 3 in Yodzis 1994), which, expanded to a multispecies framework, becomes

$$F_{ij} = \frac{C_{ij}}{1 + \sum_i h_{ij} C_{ij}} \quad (5)$$

where F_{ij} is the functional response (amount of prey i consumed by predator j per unit of time), C_{ij} is the capture rate (attack rate sensu Yodzis 1994) (the amount of prey i captured and consumed by predator j per unit of searching time), h_{ij} is the handling time per unit of prey i, and the summation in the denominator is over all prey of predator j. By using eq. 5 with different forms for C_{ij} we can build many different functional responses.

The handling time, h_{ij}, represents the amount of time that predator j spends off the search for prey because of the capture of a unit of prey i. When prey i tends towards infinity, the inverse of h_{ij} is the asymptotic maximum consumption rate (i.e., the functional response has multiple asymptotic values, one per prey species). The literal interpretation of h_{ij} as "handling" time only is too narrow; there are many other factors that can keep a predator off the search for prey because of a capture. One of the most noticeable of these is related to the physiology of the digestion process (Rindorf 2002), which allows for so-called digestive pauses (Jeschke et al. 2002). In this context, if for the sake of simplicity and to reduce the number of parameters that need to be estimated, we assume a prey-independent digestive pause (i.e., a common handling time per unit of prey for all prey of a given predator), eq. 5 can be written as

$$F_{ij} = \frac{1}{h_{ij}}\left(\frac{C_{ij}}{\frac{1}{h_{ij}} + \sum_i C_{ij}}\right) = \frac{J_j C_{ij}}{J_j + \sum_i C_{ij}} \quad (6)$$

where J_j is now a unique asymptotic maximum of the functional response of predator j. Within the bioenergetic and allometric framework (Yodzis and Innes 1992; Yodzis 1998), we estimate

$$J_j = f_{J_j} a_{J_j} w_j^{-0.25} \quad (7)$$

where f_{J_j} is the realized fraction of the physiological maximum capacity to metabolize food and $a_{J_j} w_j^{-0.25}$ represents this physiological maximum, a_{J_j} being another allometric coefficient that depends on the predator's metabolic type (Yodzis and Innes 1992; Yodzis 1998).

The precise mathematical formulations for the functional responses considered here are as follows.

The T2 functional response is derived considering

$$C_{ij} = \frac{\xi_{ij} B_i}{(Q_j + B_j)^{q_j}}$$

and is

$$F_{ij} = J_j \frac{\xi_{ij} B_i}{J_j (Q_j + B_j)^{q_j} + \sum_i \xi_{ij} B_i} \quad (8)$$

where J_j is the realized maximum capacity to metabolize food by predator j (eq. 7), B_i is the biomass of prey i, B_j is the biomass of predator j, Q_j and q_j are positive constants that define the predator-interference effect in the functional response (e.g., $q_j = 0$ corresponds to no predator interference and $Q_j = 0$ and $q_j = 1$ correspond to ratio-dependence), and ξ_{ij} is a positive constant.

The GH functional response is derived considering $C_{ij} = \gamma_{ij} B_i^{b_j}$, and is

$$F_{ij} = \frac{J_j \gamma_{ij} B_i^{b_j}}{J_j + \sum_i \gamma_{ij} B_i^{b_j}} \quad (9)$$

where γ_{ij} is a positive constant and b_j is a shape parameter ($b_j = 1$ is a Type II functional response and $b_j > 1$ is a Type III functional response).

The FD functional response is derived considering

$$C_{ij} = \frac{p_{ij} B_i^{\beta_j}}{\sum_i p_{ij} B_i^{\beta_j}} \rho_{ij} B_i$$

and is

$$F_{ij} = \frac{J_j p_{ij} \rho_{ij} B_i^{1+\beta_j}}{J_j \sum_i p_{ij} B_i^{\beta_j} + \sum_i p_{ij} \rho_{ij} B_i^{1+\beta_j}} \quad (10)$$

where p_{ij} represents the preference for prey i by predator j when all prey biomasses are equal $\left(\sum_i p_{ij} = 1\right)$, ρ_{ij} is a positive constant, and β_j is a shape parameter; $\beta_j = 0$ reduces this functional response to a multispecies Holling Type II, while $\beta_j > 0$ corresponds to a Type III functional response. Also, in the absence of alternative prey, this functional response reduces to a Type II independently of β_j, showing that any Type III-ness is caused by frequency-dependent prey preferences. This functional response has not, to the best of our knowledge, appeared elsewhere in the literature, and is under active investigation by us.

The EV functional response (Evans and Garcón 1997) can be derived considering $C_{ij} = \tau_{ij} B_i (1 + \delta_j B_i)$ and is

$$F_{ij} = \frac{J_j \tau_{ij} B_i (1 + \delta_j B_i)}{J_j + \sum_i \tau_{ij} B_i (1 + \delta_j B_i)} \quad (11)$$

where τ_{ij} is a positive constant and δ_j is a shape parameter. This functional response allows both linear and nonlinear (with a fixed exponent of 2) components in the capture rate; δ_j determines the relative weight of these components and can reduce this functional response to a multispecies Holling Type II. While most standard forms for Type III, including GH, have zero slope at the origin, this one has a finite slope there. We think of GH and EV as expressing prey refuges: "strong refuges" in the case of GH, "weak refuges" for EV. Nevertheless, this functional response was originally devised considering a "search-image" concept (G.T. Evans, Northwest Atlantic Fisheries Centre, Department of Fisheries and

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Oceans, P.O. Box 5667, St. John's, NL A1C 5X1, Canada, personal communication).

The EC functional response (Walters et al. 1997; Walters and Kitchell 2001) is

$$F_{ij} = \frac{a_{ij} v_{ij} B_i}{v'_{ij} + v_{ij} + a_{ij} B_j} \quad (12)$$

where B_i is the biomass of prey i, B_j is the biomass of predator j, and a_{ij}, v_{ij}, and v'_{ij} are positive constants. Unlike the other three functional responses, this one is not truly multispecies (i.e., the rate of predation on a given prey, i, is not affected by changes in the abundance of alternative prey). In the original Ecosim derivation (Walters et al. 1997) it was assumed that $v_{ij} = v'_{ij}$ (which is why it is common to see $2v_{ij}$ in the denominator), but in later publications (Walters and Kitchell 2001) this assumption was not kept. Considering this, and the fact that eq. 12 also provides more freedom to the functional response (i.e., more chances to obtain a good fit), we used it as presented here.

However, independently of their original derivations, the same mathematical forms can be achieved using different frameworks (Yodzis 1994), and different forms can be derived from the same ecological concept. For example, EC was motivated by the foraging-arena idea (Walters et al. 1997), but most functional-response theorists would view it as a single-species Type 0 functional response (i.e., linear and without saturation) with predator interference. In the same way, since one possible interpretation of the S-shape of Type III functional responses is the existence of prey refuges (Murdoch 1973), GH (with $b_j > 1$) can also be interpreted as another possible representation of the foraging-arena concept. Therefore, comparison of a common general model with different functional responses will provide insight into how the structure of the model affects the output and which functional forms may produce better representations of the data, but will provide no real support for any particular interpretation of the predation mechanisms involved.

The general model

The modelled system (Fig. 2) was represented by a system of four ordinary differential equations, basal equations for squid and anchovy (eqs. 13 and 14) and consumer equations for hake and sea lion (eqs. 15 and 16). Terms that represent competition (α_{ij}) were included in the squid and anchovy equations, "other mortality" terms ($-m_j B_j$) were included in the squid, anchovy, and hake equations to simulate consumption by other predators not explicitly included in the model. In the cases of hake and sea lion, which both have consumer equations, the effects of other prey sources were included by adding "other prey" terms in their functional responses, where the biomasses of these other prey were represented by positive constants. Finally, a density-dependent term ($-\mu_1 B_1^{m_1}$) was included in the sea lion equation to represent the anticipated crowding-related effects during the reproductive season, which are expected to vary strongly nonlinearly with density.

$$\frac{dB_s}{dt} = \left[r_s \frac{B_s}{K_s} (K_s - B_s - \alpha_{sa} B_a) \right] - \sum_{i=h,l} B_i F_{is} - m_s B_s - H_s \quad (13)$$

$$\frac{dB_a}{dt} = \left[r_a \frac{B_a}{K_a} (K_a - B_a - \alpha_{as} B_s) \right] - \sum_{i=h,l} B_i F_{ia} - m_a B_a - H_a \quad (14)$$

$$\frac{dB_h}{dt} = B_h \left[-T_h + \sum_{k=s,a,o} e_{hk} F_{hk} \right] - B_l F_{lh} - m_h B_h - H_h \quad (15)$$

$$\frac{dB_l}{dt} = B_l \left[-T_l + \sum_{k=s,a,h,o} e_{lk} F_{lk} \right] - \mu_1 B_l^{m_1} - H_l \quad (16)$$

where s, a, h, and l correspond to squid, anchovy, hake, and sea lion, respectively, and o represents the other prey species. This general model was fitted with the five described functional responses.

Parameterization and model evaluation

The allometry-derived parameters (a_{r_i}, a_{T_i}, a_{J_i}) were parameterized following Yodzis and Innes (1992). The remaining parameters and initial conditions were numerically fitted by minimizing the minus loglikelihood ($-\ln[\ell(\Theta)]$) between the observed and predicted biomasses. A multiplicative lognormal error structure was assumed, with the variance for each species estimated from the corresponding residuals. The $-\ln[\ell(\Theta)]$ function that was minimized for each model was

$$-\ln[\ell(\Theta)] = \sum_{i=s,a,h,l} \left\{ N_i \left[\ln(S_i) + \frac{1}{2} \ln(2\pi) \right] + \sum_{N_i} \frac{[\ln(B_{it}) - \ln(\hat{B}_{it})]^2}{2S_i^2} \right\} \quad (17)$$

where N_i is the sample size for species i, S_i^2 is the lognormal variance for species i estimated from the residuals, B_{it} is the observed biomass in year t, and $\hat{B}_{it}$ is the predicted biomass in the year t for any given species, i.

The differential equation system was solved using Gear's backward differentiation formulas (also known as Gear's stiff method (Visual Numerics 1997)), and minimization was performed using a global minimization algorithm developed by the authors (Fortran 77 subroutine, available upon request), which is based on simulated annealing ideas. During the parameter-estimation process, harvest rates (H_j) were updated annually using the corresponding annual catches. All models were written in Fortran 77.

The Akaike Information Criterion corrected for sample size (AIC_c) (Burnham and Anderson 2002) was used to rank and select the models that deserved a more thorough exploration. AIC_c was calculated as

$$AIC_c = 2\{-\ln[\ell(\Theta)]\} + 2n_p \left(\frac{N}{N - n_p - 1} \right) \quad (18)$$

where $-\ln[\ell(\Theta)]$ is the minus loglikelihood, n_p is the number of estimated parameters in the model, and N is the total sample size.

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Following Burnham and Anderson (2002) we calculated the difference between the AIC_c of each model and the lowest AIC_c (i.e., the AIC_c of the best ranked model) and used this difference (ΔAIC_c) to determine which models should be explored further. This was done by considering that all models with ΔAIC_c less than 10 deserved such exploration, while those with ΔAIC_c larger than 10 could be dismissed (Burnham and Anderson 2002).

We explored the behaviour of the selected models under different exploitation scenarios with continuation and bifurcation analysis (Doedel et al. 1991*a*, 1991*b*; Strogatz 1994), employing the AUTO 97 package (Doedel et al. 1998). This analysis allows tracking of the genesis, position, and type of equilibria, cycles, and other singular behaviours of the system, such as quasiperiodicity and chaos, while one or more parameters (the bifurcation parameters) are varied. For these analyses we expressed the harvest rate, H_j, as

$$H_j = h_j B_j \quad (19)$$

where h_j is harvesting mortality (= fishing mortality). Only equilibria and cycles were seen in our models.

We used h_j as the bifurcation parameter, and we performed four independent one-parameter bifurcation analyses for each model (one per included species). Each analysis started with the system at equilibrium and no harvest (all $h_j = 0$). From there, the h_j value of the target species was increased until its extinction or until it reached an extremely high value, while the other species were kept unexploited (i.e., $h_j = 0$ for nontarget species). In this way we were able to explore how the exploitation of any given species in the model affects the biomasses of all modelled species.

Consideration of parameter uncertainty

The use of different functional responses allows evaluation of part of the structural uncertainty. However, the behaviour of a model depends on both structure and parameters, and subtle changes in parameter values can produce significant changes in model behaviour. Therefore, to produce a more comprehensive picture we also need to address parameter uncertainty. We did this by implementing the sample–importance–resample algorithm (Punt and Hilborn 1997; McAllister and Kirkwood 1998; Gelman et al. 2000). This procedure essentially consists of creating an initial sample from an importance distribution $\tilde{\eta}(\theta)$ close to the posterior distribution $\eta(\theta)$, taking a resample from it with probabilities proportional to the importance weights $w(\theta) = \ell(\theta)\psi(\theta)/\tilde{\eta}(\theta)$, where $\ell(\theta)$ is the likelihood and $\psi(\theta)$ is the prior distribution, and using this resample $\hat{\eta}(\theta)$ as an estimate of the posterior distribution $\eta(\theta)$. The distribution $\hat{\eta}(\theta)$ is used for making inferences, calculating confidence intervals (e.g., percentile method), and so forth. A common practice is to use the prior distribution $\psi(\theta)$ as $\tilde{\eta}(\theta)$, which reduces the importance weight to $\ell(\theta)$ (Punt and Hilborn 1997).

We followed this approach using the prior distributions as $\tilde{\eta}(\theta)$ and assuming them to be uniform within the ranges defined by $\theta_{MLE} \pm 0.5\theta_{MLE}$, where θ_{MLE} indicates the parameter value corresponding to the maximum-likelihood estimator (MLE). This approach cannot be considered strictly Bayesian because we chose the range of the priors after fitting the models, but allows exploration of the joint likelihood for all parameters in the neighbourhood of its maximum.

For each model we generated an initial sample of 10 000 parameter sets and a resample of 1000. Given the number of estimated parameters, these figures only allow a coarse representation of the posterior, but this was a trade-off between the quality of the posterior representation and the limitations of computer storage and time. Considering this, and to avoid distortions in the estimation of the posterior, we used a resampling without replacement scheme to create $\hat{\eta}(\theta)$ (Gelman et al. 2000).

Using $\hat{\eta}(\theta)$, the 95th-percentile range for each parameter was obtained, and the correlations among parameters were evaluated using Spearman's rank correlation coefficient (R_S). Since multiple tests of significance for R_S were made for each model, and to keep a global level of significance $\alpha_g = 0.05$, the level of significance for each individual R_S test (α_c) was estimated as $\alpha_c = \alpha_g / n_R$, where n_R is the total number of correlation tests performed for a given model.

The effect of this parameter uncertainty on model behaviour was assessed in the following way. For each model, we selected from $\hat{\eta}(\theta)$ four parameter sets with the lowest likelihoods (i.e., the worst parameter sets) that still fell within the 95th-percentile range in parameter space. We called them extreme parameter sets, and we performed with each of them the continuation and bifurcation analyses. In this way we expected to capture some of the most extreme model behaviours that still could be considered plausible given the estimated uncertainty.

Results

Model fits

Overall, most models were able to describe reasonably well the time series for hake and sea lion, but did a poorer job with squid and anchovy (Fig. 3). In all cases, the best fits produced systems characterized by a single stable equilibrium point in the absence of harvest. The equilibrium biomasses were very similar among the EV, GH, and FD models, while those in the T2 and EC models differed, mostly that for the sea lion, which was predicted to be much lower than in the first three models (Table 1).

The squid data were, in general, poorly described, but the EV, GH, and FD models were able to capture part of the increasing trend observed in the late 1990s, while the T2 model predicted no changes and the EC model predicted a decline (Fig. 3). For anchovy, all models but T2 predicted a fairly constant population level through time; T2 predicted an increasing trend since 1980 (Fig. 3). The declining trend of the hake stock was well captured by all models, but EV, GH, and FD also predicted an increase in hake biomass associated with the harvest of sea lion in the mid-twentieth century (Fig. 3).

The sea lion trajectory was fully captured only by the EV, GH, and FD models. These models predicted a large population reduction as a consequence of the harvest, and a recovery since 1960 (Fig. 3). The T2 model was only able to predict the observed increase in sea lion abundance (Fig. 3). The EC model predicted an essentially constant sea lion biomass through time (i.e., the effects of exploitation on sea

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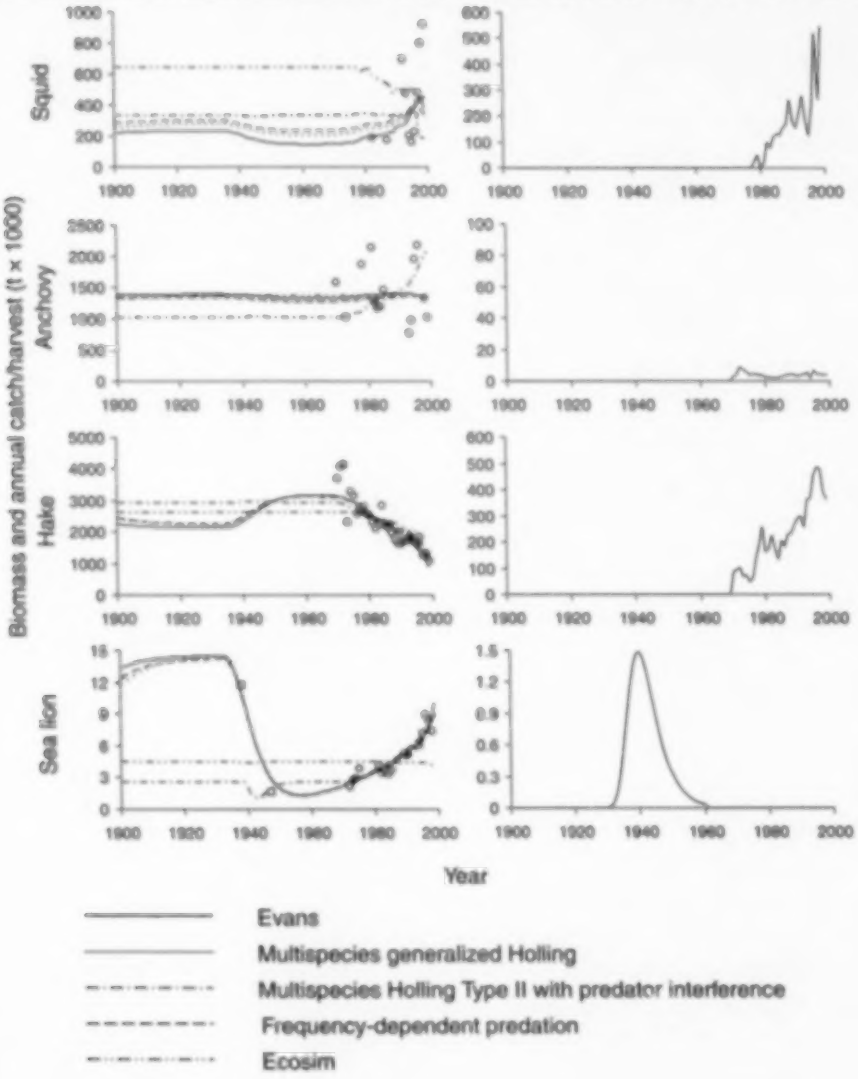
Fig. 3. Best fits of the Patagonian models. The time-series data and the best fits for the five models considered are at the left, while the annual catches for each species are at the right, showing the data used to fit the models (○). For the sea lion, two data points are indicated (□) (around 1940–1950) that correspond to earlier abundance estimates which, because of methodological differences (annual average of the censuses for a given rookery versus censuses done at the peak of the reproductive season), cannot be strictly compared with the rest of the sea lion time series. These two points were not used to fit the models, but still give an approximate idea of the sea lion population trend at that time. It is noteworthy that the Evans (EV), multispecies generalized Holling (GH), and frequency-dependent predation (FD) models were capable of capturing this sharp decline of the sea lion population, predicting values surprisingly close to these earlier abundance values. On a technical note, because the available literature on sea lion harvest reports the total number of leathers produced in 5-year periods, annual catches were estimated as the difference between consecutive years of a Gompertz function fitted to the cumulative catches (unpublished data); this is the reason for the smooth shape of the sea lion annual harvest.



lion dynamics were so slight that at the scale of Fig. 3 its dynamics appear flat-lined).

When the AIC_c values are considered, the EV model was the best and the EC model the worst (Table 1). However, ΔAIC_c indicated that only the EV and GH models were comparatively reasonable descriptions of the data (Table 1). The FD model had similar goodness of fit to the EV and GH models (Fig. 3), but because of its larger number of fitted parameters its AIC_c was substantially higher (Table 1). The T2 and EC models had clearly worse fits (Fig. 3).

Based on ΔAIC_c (i.e., <10), the EV and GH models were the only ones selected and considered worthy of further anal-

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Table 1. Comparison of the best fits among the Evans (EV), multispecies generalized Holling (GH), multispecies Holling Type II with predator interference (T2), frequency-dependent predation (FD), and Ecosim (EC) models.

	EV	GH	T2	FD	EC
n_p	40	40	42	47	50
AIC_c	1963.6	1965.7	2011.7	2073.1	2205.9
ΔAIC	0.000	2.033	48.076	109.461	242.214
Equilibrium biomasses (t) in the absence of harvest					
Squid (*Illex argentinus*)	236 228	277 135	327 827	297 302	639 411
Anchovy (*Engraulis anchoita*)	1 395 850	1 347 070	1 002 852	1 333 863	1 374 979
Hake (*Merluccius hubbsi*)	2 126 308	2 181 730	2 936 672	2 236 017	2 626 688
Sea lion (*Otaria flavescens*)	14 521	14 454	2 582	14 191	4 482

Note: n_p, number of fitted parameters.

ysis. The combination of the low ΔAIC_c (Table 1) and the similarity of the fits (Fig. 3) did not allow one model to be considered truly better than the other.

Parameter uncertainty and model behaviour

When parameter uncertainty was considered, the EV and GH models exhibited significant variability within the 95th percentile range parameter space (Tables 2 and 3). In spite of the large number of parameters being estimated, the significant correlations among them were few. For both models, when the calculated α_c level is considered, fewer than 3% of the correlations were statistically significant, and if we consider $\alpha_c = 0.05$, this figure rises to less than 11% (Tables 2 and 3).

The continuation and bifurcation analyses indicated large variability in the responses to exploitation. The range of behaviours included changes in the equilibria from point to periodic attractors (Figs. 4 and 5), and hysteresis with two basins of attractions (Fig. 4). Furthermore, even though the EV and GH models had very similar fits, they behaved quite differently in some of these exploitation scenarios.

When the EV model with the MLE parameters is considered, the harvesting of squid produced an unexpected increase and a later decrease of squid and sea lion equilibrium biomasses, hysteresis, and a region with a periodic attractor before squid extinction (Fig. 4). But the GH model had a clear negative effect on squid and sea lion from the very start of the exploitation, and a less marked effect on hake equilibrium biomass (Fig. 5). Another interesting difference between these models is observed when harvesting anchovy. This harvest has a highly negative effect on sea lion equilibrium biomass in the EV model, where sea lion even becomes extinct before anchovy (Fig. 4), while it has a positive effect in the GH model (Fig. 5).

However, there were also many similarities between these models. In a more general view, and also considering the behaviours of the extreme sets, harvesting of squid had neutral to positive effects on anchovy equilibrium biomass and neutral or slightly positive to clearly negative effects on hake equilibrium biomass, including extinction in some cases (Figs. 4 and 5). The effects on sea lion equilibrium biomass ranged from neutral to clearly negative and extinction (Figs. 4 and 5), although they also included the positive effect at intermediate h_s values and the hysteresis behaviour described above for the best fit (MLE parameters) of the EV model (Fig. 4).

Exploitation of anchovy had neutral to clearly positive effects on squid equilibrium biomass and neutral to clearly negative effects on hake equilibrium biomass (Figs. 4 and 5). In the case of the sea lion, the anchovy harvest produced virtually all possible effects, including clearly positive, neutral, clearly negative, and extinction ((Figs. 4 and 5).

The harvesting of hake led in many cases to exploited systems with limit-cycle behaviour at intermediate levels of exploitation. This limit-cycle behaviour was absent in the EV-model best fit (Fig. 4) but present in the GH-model best fit. In both models the hake harvest had a clearly positive effect on squid, while the characteristic effect on anchovy equilibrium biomass was clearly negative at high levels of exploitation, but sometimes neutral or positive at low and (or) intermediate levels of exploitation (Figs. 4 and 5). Sea lion presented an interesting result when harvesting hake. The best fits for both models showed a clear positive effect on sea lion equilibrium biomass, but all extreme sets showed clearly negative effects, including extinction (Figs. 4 and 5).

The harvesting of sea lion had neutral to negative effects on squid equilibrium biomass, virtually neutral effects on anchovy, and neutral to positive effects on hake (Figs. 4 and 5).

Discussion

Our results indicate large variability with respect to both model structure (i.e., different functional responses) and parameter uncertainty. Even the behaviour of the selected models (EV and GH), which also had very similar best fits, differed substantially in some exploitation scenarios. This indicates that model uncertainty is a factor that cannot be dismissed if we want to use simple models to gain insight into the dynamics of much more complex systems such as actual marine communities. The observed variability largely agrees with previous results obtained from local dynamic models of higher complexity (Yodzis 1998, 2000), and suggests that achieving management-quality multispecies models can be even harder than is generally thought. Fortunately, in spite of this variability, it was still possible to reach some coarse-grain conclusions. Given the extent of model uncertainty explored in these analyses, we expect these emerging patterns to be robust to a fairly wide range of structure and parameter uncertainty. The sample and resample sizes used for the implementation of the sample–importance–resample algorithm were small for models of these sizes (e.g., see Givens et al. 1993), but this was imposed by hardware limi-

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Table 2. Maximum-likelihood estimators (MLE) and 95th-percentile ranges (A) and correlations among parameters (B) for the EV functional response model.

(A) MLEs and 95th-percentile ranges.

Parameter	MLE (best fit)	95th-percentile range	Parameter	MLE (best fit)	95th-percentile range
f_{v_1}	0.93260	0.53091to 0.99353	τ_{sl}	0.08178	0.04214 to 0.09826
f_{v_2}	0.92857	0.47808 to 0.98425	τ_{al}	0.00167	0.00087 to 0.00245
K_s	2 853 523	1 563 293 to 4 226 968	τ_{hl}	0.08572	0.04429 to 0.09875
K_a	2 145 852	1 343 419 to 3 177 336	τ_{cl}	0.03120	0.01634 to 0.04597
α_{sa}	2.97×10^{-10}	1.54×10^{-10} to 4.34×10^{-10}	e_{sh}	0.54976	0.54021 to 0.82099
α_{ss}	0.88012	0.45847 to 1.28900	e_{ah}	0.60702	0.50689 to 0.89731
m_s	0.44936	0.23514 to 0.66297	e_{ch}	0.35681	0.18901 to 0.50492
m_a	2.26988	1.17435 to 3.31945	e_{sl}	0.77471	0.50913 to 0.94185
m_h	0.87788	0.45736 to 1.28366	e_{al}	0.91288	0.50871 to 0.93609
μ_l	1.95×10^{-14}	1.01×10^{-14} to 2.87×10^{-14}	e_{hl}	0.72435	0.67855 to 0.94442
v_l	3.969	2.773 to 5.458	e_{cl}	0.37713	0.20046 to 0.55769
f_{sh}	0.85387	0.52065 to 0.97779	B_{sh}	879 142	501 497 to 1 299 200
f_{ah}	0.85275	0.70718 to 0.99681	B_{sl}	316 166	166 923 to 463 967
δ_0	2.53348	1.32795 to 3.73444	t_0	1849.74	1848.03 to 1849.84
δ_1	1.90571	1.04749 to 2.81641	B_{s0}	527 754	273 690 to 781 512
τ_{sh}	0.13283	0.06806 to 0.19547	B_{a0}	1 235 718	927647 to 1 821 393
τ_{ah}	0.00342	0.00179 to 0.00508	B_{h0}	1 767 966	1 526 734 to 2 608 530
τ_{ch}	0.04768	0.02605 to 0.07058	B_{l0}	2350	1 224 to 3 480

(B) Correlations among parameters.

	No.	Percentage
R_S with $p < 0.05$	63	10.0
R_S with $p < \alpha_c$	14	2.2
n_R	630	
α_c	7.94×10^{-5}	

Detailed correlations with $p < \alpha_c$

Parameters		R_S	p
f_{v_1}	K_s	–0.134	2.22×10^{-5}
f_{v_1}	τ_{sh}	–0.156	7.18×10^{-7}
f_{v_1}	τ_{ah}	0.182	6.48×10^{-9}
f_{v_1}	B_{sh}	–0.131	3.09×10^{-5}
K_a	e_{sh}	–0.140	8.35×10^{-6}
e_{sh}	f_{sh}	–0.449	0.00
τ_{sh}	B_{sh}	–0.162	2.41×10^{-7}
e_{sh}	f_{sh}	–0.263	3.00×10^{-17}
τ_{sh}	B_{sh}	0.138	1.27×10^{-5}
m_h	f_{sh}	0.248	1.66×10^{-15}
e_{cl}	v_l	0.125	7.29×10^{-5}
e_{hl}	v_l	0.167	1.01×10^{-7}
e_{hl}	f_{sh}	–0.378	2.88×10^{-35}
v_l	f_{sh}	0.295	1.68×10^{-21}

tations (essentially not enough hard drive to handle initial samples 100–1000 times larger than the ones used here). Therefore, our parameter-uncertainty assessment is an approximation; we do not claim that we have fully estimated the posterior distributions. However, this approximation produces a broader $\hat{\eta}(\Theta)$, which leads to larger 95th-percentile ranges. Therefore, in terms of any conclusions drawn from these results, an improved assessment of parameter uncertainty should only narrow the range of uncertainty and, hence, make such conclusions more precise.

Regarding the best fits, one interesting point is the dynamic between hake and sea lion and the prediction that hake was above its equilibrium biomass when its fishery started. Even though this feature is not common to all models, its presence in the two selected ones suggests that it might have been an actual event in the history of the Patagonian marine system. Therefore, the assumption that hake was at equilibrium when the fishery started, which is a classic and common one in many single-species models (e.g., carrying capacity, virgin biomass, etc), is not supported by our results. Furthermore, this also suggests that using the early-1970s biomass estimates for establishing recovery targets or estimating reference points may be misleading and potentially dangerous. Such an assumption implies that the virgin system could have supported a higher biomass of hake than it actually did, at least according to our results.

The squid and anchovy data were poorly described by the models. However, the lack of ability to accurately describe the dynamics of these species is not a surprise. The squid has an annual life cycle (Brunetti et al. 1999*a*), and the an-

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Table 3. MLEs and 95th-percentile ranges (A) and correlations among parameters (B) for the GH functional response model.

(A) MLEs and 95th-percentile ranges.

Parameter	MLE (best fit)	95th-percentile range	Parameter	MLE (best fit)	95th-percentile range
f_{c_1}	0.86801	0.47524 to 0.99484	γ_{cl}	0.08815	0.04558 to 0.09837
f_{c_2}	0.91720	0.47417 to 0.98718	γ_{sl}	0.00223	0.00117 to 0.00329
K_c	3 321 734	1 792 058 to 4 911 329	γ_{hl}	0.09125	0.04690 to 0.09808
K_s	2 115 283	1 327 527 to 3 152 055	γ_{cl}	0.02900	0.01523 to 0.04268
α_{sc}	2.94×10^{-10}	1.55×10^{-10} to 4.30×10^{-10}	e_{ch}	0.55677	0.52123 to 0.83124
α_{cc}	0.97352	0.50919 to 1.41657	e_{sh}	0.59805	0.51342 to 0.88708
m_c	0.55805	0.29021 to 0.82107	e_{ch}	0.35553	0.19197 to 0.50765
m_s	1.76599	0.92432 to 2.60231	e_{sl}	0.82626	0.51004 to 0.94046
m_h	0.84649	0.44126 to 1.24463	e_{sl}	0.80062	0.51289 to 0.94019
μ_1	8.36×10^{-15}	4.36×10^{-15} to 1.24×10^{-14}	e_{hl}	0.72923	0.67965 to 0.94534
ν_1	4.057	2.878 to 5.491	e_{cl}	0.21560	0.11356 to 0.31836
f_{ch}	0.84003	0.50647 to 0.98389	B_{ch}	865 321	470 852 to 1 278 300
f_{sh}	0.84781	0.70789 to 0.99600	B_{sl}	315 445	167 619 to 465 319
b_h	2.53443	1.74561 to 3.75372	t_0	1 849.84	1848.05 to 1849.86
b_1	1.96523	1.03098 to 2.90281	B_{cl}	523 108	271 218 to 765 839
γ_{ch}	0.14702	0.07662 to 0.21588	B_{sl}	1 144 109	920 713 to 1 692 595
γ_{sh}	0.00238	0.00125 to 0.00351	B_{hl}	1 856 502	1 549 210 to 2 756 074
γ_{ch}	0.03735	0.01955 to 0.05516	B_{ini}	1 358	1028 to 2007

(B) Correlations among parameters.

	No.	Percentage
R_S with $p < 0.05$	68	10.8
R_S with $p < \alpha_c$	12	1.9
n_R	630	
α_c	7.94×10^{-5}	

Detailed correlations with $p < \alpha_c$		
Parameters	R_S	p
f_{c_1} e_{ch}	−0.129	4.17×10^{-5}
f_{c_1} b_h	−0.154	1.02×10^{-6}
K_c f_{sh}	−0.141	7.15×10^{-6}
e_{ch} m_h	0.127	5.70×10^{-5}
e_{ch} f_{sh}	−0.513	0.00
e_{sh} f_{sh}	−0.297	7.18×10^{-22}
γ_{sh} b_h	0.153	1.15×10^{-6}
b_h B_{ch}	−0.227	3.93×10^{-13}
m_h f_{sh}	0.227	3.75×10^{-13}
e_{hl} ν_1	0.172	4.47×10^{-8}
e_{hl} f_{sh}	−0.344	3.09×10^{-20}

chovy, like many other forage fish, is known to have large fluctuations in abundance (Ciechomski and Sánchez 1988; Hansen and Madirolas 1996; Hansen 1999). Both species are considered highly susceptible to environmental factors (Ciechomski and Sánchez 1988; Brunetti et al. 1999*a*; Hansen 1999), and no environmental effects were included in these models. Regarded in this light, our fits do not appear to be that bad. Furthermore, the selected models were still capable of capturing some of the observed increase in squid in the late 1990s. This suggests that the increase, or at least part of it, could be related to the interplay between trophodynamics and exploitation.

In approaches like the one implemented here, the scarcity of data usually leaves very little room for model validation, since all available data are typically used for fitting purposes. Our case is no exception: we used the whole database for fitting the models. However, we did not use any quantitative diet or consumption data; the model predicts this information for any given functional response and parameter set. We can compare consumption by hake and sea lion estimated in this way with any available consumption information. In our case, this cannot constitute formal model validation, but it allows the comparison of some model predictions with fairly independent estimates of the same variables. Furthermore, using $\hat{\eta}(\theta)$ we can build distributions for these variables and obtain their 95th-percentile ranges.

Total trophic consumption by hake was estimated for the period 1970–1986 (Prenski and Angelescu 1993). Because this estimate included both the Bonaerensis and the Patagonian hake stocks (Prenski and Angelescu 1993), we cannot compare consumption estimates directly. However, considering that the Patagonian stock represents more than 80% of the combined biomass, the comparison is still a useful guideline. Like their fits, the consumption estimates from both models were very similar (Table 4). The models estimated more squid and less anchovy consumption by hake than in the previous study, although the 95th-percentile ranges overlapped and included the previous estimate (Table 4).

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Fig. 4. Bifurcation analyses for the EV model. Each quadrant corresponds to the bifurcation analysis that considers the harvesting of one species at a time, where the analysis starts with the system at equilibrium and no harvest and ends when the harvested species goes extinct. In each quadrant, the graphs at the left correspond to the maximum-likelihood estimators (MLE) of the parameters (best fit) and those at the right to the extreme parameter sets. The solid lines indicate stable equilibrium points, while the dotted lines indicate unstable ones. In the MLE diagrams, periodic attractors (cycles) are represented by two lines (pitchfork shape), which indicate the amplitude of the cycle for the corresponding harvesting mortality. In the graphs representing the extreme parameter sets, the periodic attractors are indicated with very close solid circles (thick lines), without an indication of the amplitude of the cycles. For visualization purposes, some extreme-set graphs have a secondary y axis; arrows indicate the graphs that should be read on these secondary axes.

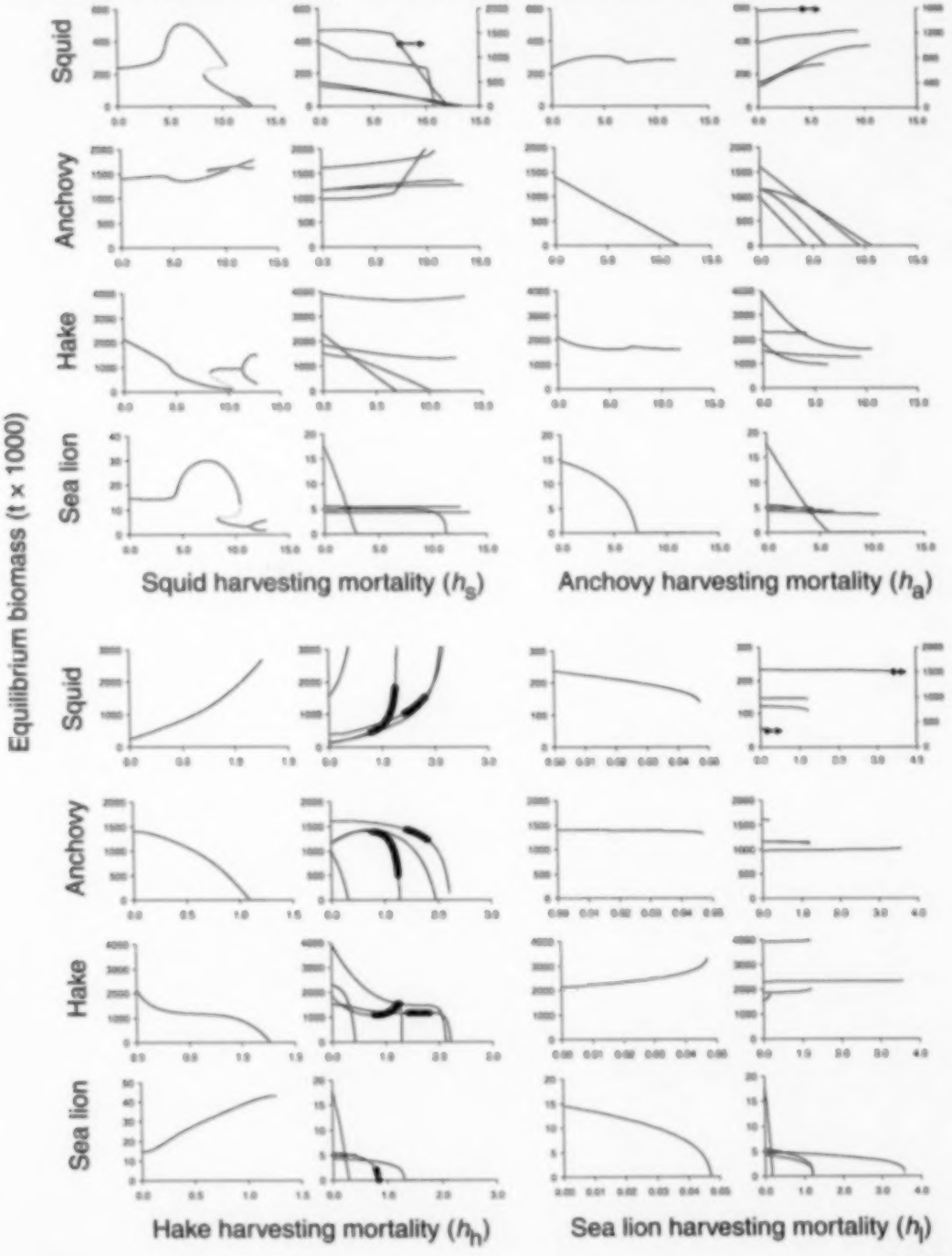

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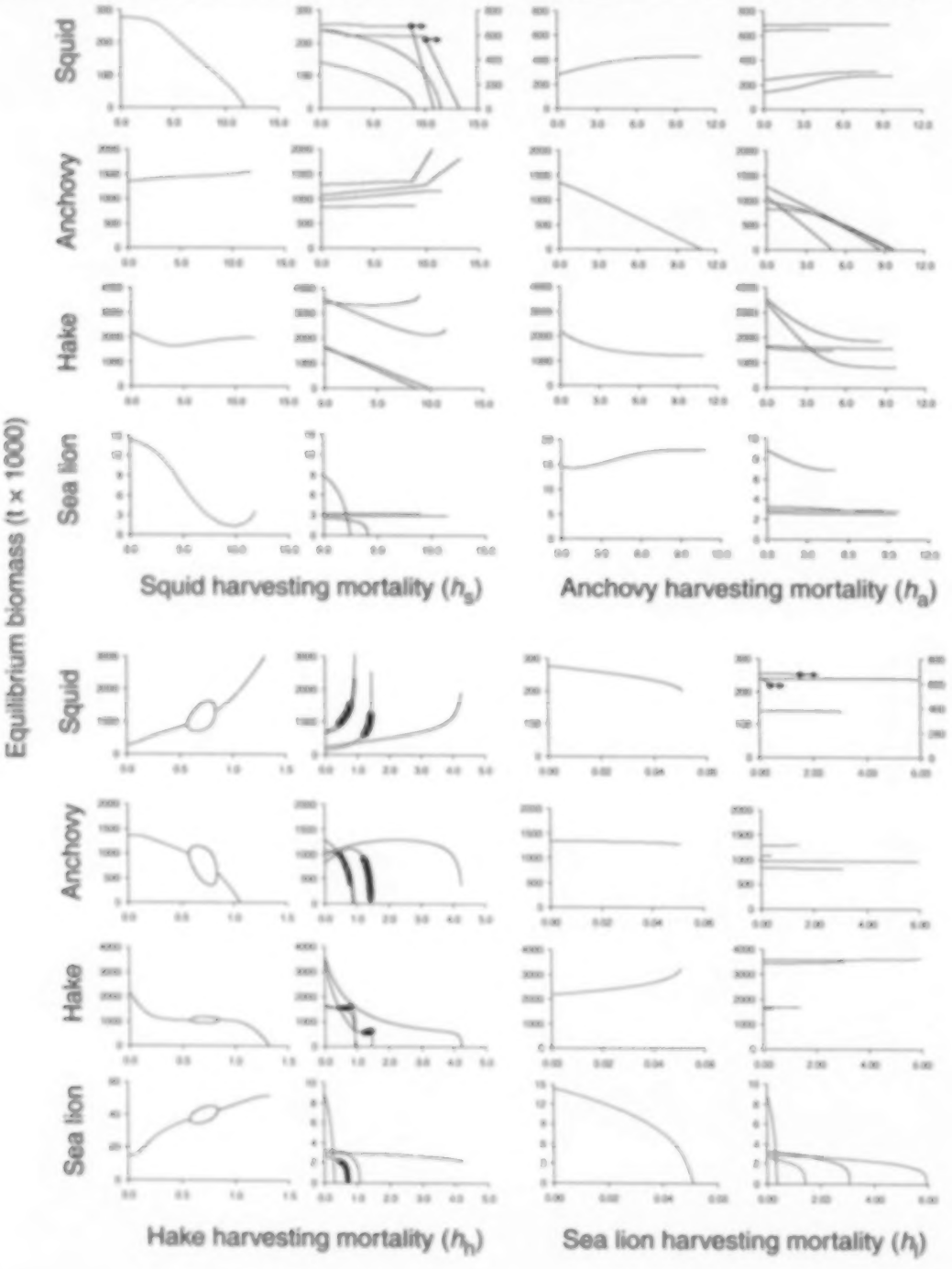
Fig. 5. Bifurcation analyses for the GH model. Each quadrant corresponds to the bifurcation analysis that considers the harvesting of one species at a time, where the analysis starts with the system at equilibrium and no harvest and ends when the harvested species goes extinct. In each quadrant, the graphs at the left correspond to the MLEs of the parameters (best fit), and those at the right to the extreme parameter sets. The solid lines indicate stable equilibrium points. In the MLE graphs, periodic attractors (cycles) are represented by two lines (i.e., defining a bubble-shaped structure in the graph), which indicate the amplitude of the cycle for the corresponding harvesting mortality. In the extreme-set graphs, the periodic attractors are indicated with very close solid circles (thick lines), without an indication of the amplitude of the cycles. For visualization purposes, some extreme-set graphs have a secondary *y* axis; arrows indicate the graphs that should be read on these secondary axes.



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Similarly, when estimates of total hake consumption were compared, those from the models were also higher, but again the 95th-percentile ranges overlapped and included the previous value (Table 4).

In the case of sea lion, the other consumer in these models, the only available estimate of consumption by the population corresponds to the population estimated for 1996, but the diet information used in this analysis was collected during the 1990s (Koen-Alonso et al. 1999). This estimate was based on individual consumption rates (Innes et al. 1987) and diet composition from stomach-content analysis (Koen-Alonso et al. 2000*a*), and included a bootstrap procedure to incorporate the variability in diet composition (Koen-Alonso et al. 1999). We compared this information with the average annual consumption rates for the period 1990–1999 obtained from the models. Here, as in the case of hake, we also found extremely wide 95th-percentile ranges, which overlapped between models and previous estimates (Table 4). The squid and anchovy consumption rates from the models were very close to previous estimates, but hake consumption from both models was more than double the previous estimate (Table 4). Total prey-consumption rates were also very similar, but this is not completely unexpected, since the individual consumption rate in the earlier study (Koen-Alonso et al. 1999) and the maximum consumption rates in our models had allometrically derived elements (Innes et al. 1987; Yodzis and Innes 1992).

However, at the level of individual prey the consistency between previous consumption estimates and the models' predictions is truly remarkable (all of them are of the same order of magnitude and within a factor of less than 3 of each other). In our models, the consumption predictions are by-products of the modelling approach; estimation of consumption is not the main goal. Still, comparisons like these are very valuable for model validation. More precisely, they are useful for cross-checking models, since consumption estimates are always the result of different kinds of modelling exercises. In our case, the observed high level of consistency improves the odds of capturing some reality in these modelling attempts, but the best models still picture the sea lion as a much more severe hake predator than the few available quantitative diet data suggest (Koen-Alonso et al. 2000*a*). However, given the typically large uncertainty in estimates of pinniped diet composition and consumption (e.g., Shelton et al. 1997), this difference really indicates that we still have a poor understanding of sea lions' food habits.

Although these models were not intended as management tools, the patterns in the predicted equilibrium biomasses under different exploitation scenarios are still of some use for fishery management. These patterns refer to the equilibrium biomasses of the system, not to the transient behaviour that will bring the system to these equilibrium states (Strogatz 1994). In most applied cases the transient behaviours are likely to be as important as the equilibria themselves because it may take the system a very long time to reach equilibrium (Hastings 1996). Nevertheless, we can still regard these patterns as a road map for the system's response to the exploitation of its individual components.

Within this context, for example, we can say that fishing anchovy will have a negative impact on hake. Since from a single-species perspective the anchovy is considered underexploited (Hansen 1999), after the hake stocks collapsed, interest in developing an anchovy fishery as a palliative measure increased (Crespo et al. 2000). Since 2002 there has been an ongoing project within the agency in charge of fishery management in Chubut Province (one of the Patagonian provinces in Argentina) to explore and develop this alternative fishery. Based on our results, such a fishery would likely reduce the chances of hake recovery. In this context, one unexpected prediction arises from considering the effect of the hake fishery on anchovy. Our analysis indicates that high fishing mortalities for hake have a strong negative impact on the equilibrium biomass of anchovy. Despite the poor fits that we obtained for anchovy, it is noteworthy that Hansen and Madirolas (1996) had already discussed their own perceptions that anchovy was showing signs of a decline in abundance. At that time they were not sure if the available evidence was showing a negative trend or just low values within the natural limits of variation, but in view of the hypothesis of a decline, they were wondering how such an observation could be consistent with the decline in hake, its most important predator (Hansen and Madirolas 1996). With all their limitations, it is still very interesting that our models predict this counterintuitive behaviour and provide some insights into the possible causes of such a trend (e.g., competition with squid).

Regarding ways for promoting hake recovery, the culling of sea lions may at first glance seem a possibility. This option has never been seriously considered; sea lions are currently protected by federal law in Argentina and they also constitute one of the core attractions for tourism, which is a growing industry in Patagonia (Tagliorete and Losano 1996). Within our models, culling sea lions can have a positive effect on hake, but in the same cases it has an equally important negative effect on squid. This means that a management strategy of culling sea lions for the sake of the hake fishery would hinder the squid fishery at the same time.

Our results also indicate that the hake fishery might have had a boosting effect on squid, while the squid fishery may reduce the chances of hake recovery. Putting all of this together, even though this is just an exploratory modelling exercise, if we think in terms of a large squid fishery and a potential anchovy fishery, our results clearly suggest that these activities may hinder and (or) delay the rebuilding of the hake stock.

From the point of view of tourism, our results also suggest that the hake fishery does not necessarily have a strong negative effect on sea lions. In both models, the bifurcation analyses considering the maximum-likelihood parameters (i.e., the most likely response) indicated that the hake fishery actually boosts the sea lion equilibrium biomass, but the extreme sets also showed the opposite result, including sea lion extinction. Obviously, there is no robust prediction here, and further research is needed to clarify this issue, but the fact that despite the collapse of the hake stocks, the sea lion population is still recovering (Dans et al. 2004), together with the most likely behaviours derived from our models, suggests as a working hypothesis that the odds in favour of a strong negative impact of the hake fishery on sea lions are low. Nevertheless, this conclusion is based only on the trophodynamic relationships included in the models and does not consider the effects of by-catch.

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Table 4. Average annual food consumption ($t \cdot year^{-1}$) by hake and sea lion during the periods 1970–1986 and 1990–1999, estimated by the EV and GH models and from other available studies.

	EV model	GH model	Other sources[a]
1970–1986			
Squid consumed by hake	2 076 561 (753 042 – 8 520 710)	2 499 038 (1 020 219 – 8 203 621)	1 921 720
Anchovy consumed by hake	3 240 981 (180 906 – 6 280 130)	3 293 086 (165 552 – 6 712 025)	4 050 223
Total consumption by hake	24 066 767 (9 426 029 – 29 481 974)	23 705 215 (10 389 546 – 29 242 748)	14 706 268
Squid consumed by sea lion	367 (65 – 42 662)	653 (67 – 46 667)	
Anchovy consumed by sea lion	402 (126 – 6787)	472 (121 – 6 424)	
Hake consumed by sea lion	72 026 (37 039 – 341 867)	71 894 (39 465 – 298 953)	
Total consumption by sea lion	73 191 (39 520 – 402 496)	73 384 (43 175 – 327 160)	
1990–1999			
Squid consumed by hake	3 487 760 (775 192 – 8 684 187)	3 413 595 (993 785 – 8 621 463)	
Anchovy consumed by hake	1 598 598 (104 302 – 5 552 358)	1 748 327 (100 781 – 6 470 734)	
Total consumption by hake	13 937 979 (8 157 653 – 22 448 813)	13 853 080 (8 739 301 – 24 034 533)	
Squid consumed by sea lion	8 191 (154 – 48 598)	9 522 (175 – 45 217)	13 900 (3709 – 30 829)
Anchovy consumed by sea lion	2 331 (175 – 7 609)	2 873 (226 – 7 499)	2 410 (52 – 8 778)
Hake consumed by sea lion	139 540 (30 543 – 250 614)	138 270 (34 440 – 227 214)	51 260 (30 074 – 76 786)
Total consumption by sea lion	152 345 (36 545 – 268 714)	152 785 (40 984 – 252 430)	148 325

Note: The values provided for the models correspond to the best fit. Values in parentheses show the 95th-percentile range from $\hat{\eta}(\theta)$.

[a]The information on hake consumption for the period 1970–1986 was estimated for the two hake stocks in Argentine waters, the Bonaerensis and the Patagonian stocks (Prenski and Angelescu 1993). The models developed in this paper only deal with the Patagonian stock. However, the Patagonian stock is the largest one, representing 80% or more of the joint biomass. For the period 1990–1999, the information on sea lion consumption was obtained from Koen-Alonso et al. (1999). These estimates were obtained from mean individual consumption rates (Innes et al. 1987) and diet information. In this case, the values in parentheses are the 95% confidence intervals obtained by a bootstrap procedure. This bootstrap analysis only considered the variability in stomach-content composition (Koen-Alonso et al. 1999).

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Table 5. Comparison of the effects of harvesting on equilibrium biomasses between predictions based on biological common sense and from the bifurcation analyses of the EV and GH models.

	Harvesting of:			
Effect on:	Squid	Anchovy	Hake	Sea lion
(A) Predicted effects based on biological common sense				
Squid (*Illex argentinus*)	–	+	+	+
Anchovy (*Engraulis anchoita*)	+	–	+	+
Hake (*Merluccius hubbsi*)	–	–	–	+
Sea lion (*Otaria flavescens*)	–	–	Unknown	–
(B) Synthetic view of the results from the EV and GH models[a]				
Squid				
EV	[–] (–)	[–] (+)	[+] (+)	[–] (–)
GH	[–] (–)	[+] (+)	[+] (+)	[–] (0/–)
Anchovy				
EV	[–] (+)	[–] (–)	[–] (–/–)	[–] (0/+)
GH	[+] (+)	[–] (–)	[–] (–/–)	[–] (0/+)
Hake				
EV	[–] (–/–)	[–] (–)	[–] (–/–)	[+] (+)
GH	[–] (–/–)	[–] (–)	[–] (–/–)	[+] (+/0)
Sea lion				
EV	[–] (–/0)	[–] (–)	[+] (–)	[–] (–)
GH	[–] (–/0)	[+] (–)	[+] (–)	[–] (–)
(C) Agreement between biological common sense predictions and models results[b]				
Squid	PA	PA	A	D
Anchovy	PA	A	PD	PD
Hake	PD	PA	PA	A
Sea lion	PA	PA	na	A

[a]Symbols in brackets correspond to the results from the best fits (i.e., the most likely effects), while symbols in parentheses indicate the results from the "extreme" sets: +, positive effect; –, negative effect; –, non-monotonic effect (i.e., the sign of the effect depends on the value of the harvesting mortality); 0, neutral effect. For the extreme sets, the slash (/) indicates that more than one type of effect was observed, and the order of the symbols roughly indicates their order of importance.

[b]A, agreement; D, disagreement; PA, partial agreement; PD, partial disagreement; na, not applicable.

These general conclusions largely agree with the results of a previous attempt at modelling this system (Koen-Alonso et al. 2000*b*; Dans et al. 2003). This earlier model was rudimentary and based on a completely different theoretical framework (Berryman et al. 1995), but its results also indicated that the fishing of squid hindered the recovery of hake, and sea lion showed an increasing trend in spite of the increase in fishing catches (Koen-Alonso et al. 2000*b*; Dans et al. 2003), thus adding to the robustness of those predictions.

The simplest model possible is the conceptual one that we build using biological common sense. Such common sense typically considers only the most direct links between components in a system and dismisses the effect of longer pathways in the food web (e.g., harvesting a predator has a positive effect on its prey; harvesting one competitor has a positive effect on the other). Therefore, we can compare these conceptual models based on biological common sense with the results obtained from our models to determine if biological intuition can be a reasonable "minimum-realistic" model of these simple food-web models.

In our study, such an analysis shows that in some cases there is full agreement, but it also reveals one case of complete disagreement between our biological intuition and the models (Table 5). However, the most remarkable result is that in most cases the agreement or disagreement is only partial (Table 5), and many of them involve non-monotonic responses to exploitation (Table 5). This result, given also the extremely simplified trophic structure of our models, clearly undermines our self-confidence about our own ability to integrate and incorporate multispecies effects without explicit modelling of such relationships.

It is well known that long-term effects of exploitation are largely structurally undetermined (i.e., whether species' responses to exploitation are positive or negative is not governed by food-web topology alone), and we need to know the precise values of the parameters (and their variability) in order to predict the responses (Yodzis 1988). However, non-monotonic responses are somehow less present in our thoughts, even though they have been already pointed out as a possible theoretical output (Yodzis 1996). The meaning of this type of response is that the effect of exploitation on a given species not only will vary in magnitude with the exploitation rate, but also can change in sign. Depending on the harvest rate, the response can be positive or negative even for the very species being harvested (e.g., fishing squid in the EV model).

From a modelling perspective, several points are noteworthy. The two models that performed best, EV and GH, shared a laissez-faire (i.e., predator-independent) Type III-shaped functional response. This is interesting because there is ap-

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parent consensus among many ecologists that the most common functional responses are Type II (e.g., Jeschke et al. 2002). However, many of these observations come from laboratory experiments where, typically, one predator is faced with one prey (e.g., Murdoch 1969). When more than one prey is present, is not unusual to observe Type III functional responses (e.g., Holling 1959). Early on it was clear that very simple biological processes such as prey switching, the presence of prey refuges, or predator learning had the potential to transform an initial Type II functional response into a Type III (Murdoch 1973), and Type III shapes have been observed in switching experiments (e.g., Murdoch 1969; Murdoch et al. 1975). Furthermore, Type III functional responses are frequently used to implicitly model prey switching (Chesson 1983; van Baalen et al. 2001), and have the property of stabilizing predator–prey systems (Oaten and Murdoch 1975). This form is also the phenomenological result of explicitly modelling prey switching with underlying Type II functional responses (Post et al. 2000; our FD model), and is also the expected emergent shape from weak-link interactions (McCann 2000).

The functional response that performed the worst was the Ecosim formulation. The EC model also produced different results from the two best performing functional responses in a bifurcation analysis like the ones presented here. This is disturbing in view of the widespread and uncritical use of the Ecopath with Ecosim package. Fishery modellers are accustomed to carefully scrutinizing parameter estimates. As we move into the new realm of multispecies modelling, we need to recognize that the nonlinear mathematical structures of these models (encapsulated here in the functional response) need to be treated with the same care as parameters.

Food-web models are usually closed (i.e., the modelled system is assumed to be closed) and typically ignore any form of resource competition among basal species. In our case we kept the system open at the prey field level for the consumer species by including alternative prey to the modelled ones. These other prey sources were simply constant prey biomasses available to the predators, but their incorporation avoided the unrealistic assumption that the predators only fed upon the species explicitly included in the model. The other factor that we incorporated was a competitive effect between the basal species. This incorporation greatly improved the performance of our models, but in a more general sense this kind of competition is likely to be very common in nature. These features, although still rudimentary, enhance the representation of those inputs from the rest of the community that are affecting the behaviour of the modelled subsystem.

From an applied perspective, we prefer to see our results as a glass half-full rather than half-empty. In spite of all the variability and complexity, this work shows that there are reasonable ways to address the issues, putting us closer to management-quality multispecies models. Furthermore, the approach implemented here circumvents the problem of uncertainty in quantitative diet composition by making model parameterization less reliant on this source of information, and, at the same time, freeing available data for model validation. Finally, our approach shows how to cope with the fact that predictions from models with different functional responses can vary substantially, though more work in this direction is needed. At the very least, we have clearly demonstrated that a single model structure cannot be considered per se a reliable source for making inferences about the modelled system.

Addendum

Peter Yodzis passed away on 28 March 2005, while this paper was in press. As scientists we will all miss his insights and clarity of thought; as a friend I will always miss his deep laugh and unbounded generosity. Until the next time, my friend.

Mariano Koen-Alonso

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Appendix A

Table A1. Database of biomasses and catches for squid (*Illex argentinus*), anchovy (*Engraulis anchoita*), hake (*Merluccius hubbsi*), and sea lion (*Otaria flavescens*) used for the fitting of the models presented in this paper.

	Biomass (t)				Catch (t)			
Year	Squid	Anchovy	Hake	Sea lion	Squid	Anchovy	Hake	Sea lion
1929								0.15
1930								1.72
1931								11.23
1932								47.28
1933								140.45
1934								316.15
1935								570.92
1936								865.72
1937								1143.12
1938								1352.97
1939								1468.73

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Table A1 (*concluded*).

	Biomass (t)				Catch (t)			
Year	Squid	Anchovy	Hake	Sea lion	Squid	Anchovy	Hake	Sea lion
1940								1489.25
1941								1430.93
1942								1317.77
1943								1173.65
1944								1018.12
1945								865.06
1946								723.10
1947								596.70
1948								487.44
1949								395.03
1950								318.13
1951								254.94
1952								203.51
1953								161.96
1954								128.58
1955								101.89
1956								80.61
1957								63.71
1958								50.30
1959								39.69
1960								31.30
1970		1 589 287	3 700 000		69	2881	87 400	
1971			4 094 920		96	4346	92 000	
1972			4 140 564	2110	94	8685	102 800	
1973		1 020 100	2 300 000	2691	331	7264	70 400	
1974			3 286 369	2903	441	6429	74 200	
1975			3 149 437	3860	390	4051	50 000	
1976			2 600 000		927	4320	60 906	
1977			2 642 715		143	4605	134 848	
1978		1 892 045	2 823 409		23 638	3406	189 161	
1979			2 634 311		50 702	4199	255 905	
1980			2 562 585		5 944	2263	162 350	
1981		2 151 767	2 308 283	4140	14 401	2620	174 729	
1982	192 600	1 285 930	2 099 625	3487	96 925	2136	223 909	
1983		1 188 776	2 230 037	3780	80 058	2237	176 100	
1984		1 203 181	2 842 969	3305	120 772	2050	135 224	
1985		1 480 093	2 203 954	3720	133 166	2583	203 334	
1986			2 142 882		127 970	3323	182 858	
1987	181 977		1 960 388		155 681	4097	230 325	
1988			1 779 005		169 213	4117	233 526	
1989			1 639 150	5248	262 978	4384	263 533	
1990			1 643 631	5210	180 767	2771	288 398	
1991			1 737 620		155 681	4360	297 079	
1992	693 538		1 722 591		214 414	4080	255 369	
1993	479 571	764 710	1 836 000		277 622	5729	364 928	
1994	203 820	975 298	1 775 049	6084	185 403	2123	365 695	
1995	168 943	1 969 881	1 654 398	7146	129 093	6530	457 306	
1996	225 602	2 198 822	1 819 739	8897	244 617	4546	487 356	
1997	483 532		1 252 698	8428	523 341	4189	480 452	
1998	799 641	1 327 565	1 342 216	7407	267 255	4301	392 463	
1999	921 254	1 025 945	1 086 010		546 303	4301	365 000	

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Appendix B

Table B1. List of symbols with their corresponding unit(s), where not dimensionless, and a brief description.

Symbol	Unit(s)	Description
N_i	Dimensionless	Total number of biomass estimates for species i contained in the database
B_i	tonne	Biomass of species i
r_i	year^{-1}	Intrinsic biomass/production ratio of species i
K_i	tonne	Carrying capacity of species i
α_{ij}	Dimensionless	Competition coefficient of species j on species i
F_{ij}	year^{-1}	Functional response of species j preying on species i
m_i	year^{-1}	"Other mortality" rate of species i
H_i	tonne·year^{-1}	Harvest rate of species i
f_{ε_i}	Dimensionless	Fraction of its maximum physiological capacity for production realized by species i
a_{ε_i}	year^{-1}·kg$^{0.25}$	Allometric coefficient of the maximum physiological capacity for production of species i. It depends on species i's metabolic type
w_i	kg	Mean individual biomass of species i
T_i	year^{-1}	Mass-specific respiration rate of species i
e_{ij}	Dimensionless	Assimilation efficiency by species j of prey i
μ_i	year^{-1}·tonne$^{(1-\nu_i)}$	Density-dependent mortality coefficient of species i
ν_i	Dimensionless	Density-dependent mortality exponent of species i
a_{T_i}	year^{-1}·kg$^{0.25}$	Allometric coefficient of the mass-specific respiration rate of species i; it depends on species i's metabolic type
C_{ij}	time^{-1}	Generic capture rate, i.e., consumption of species i by predator j per unit of j searching time
h_{ij}	time	Generic handling time, i.e., time spent by predator j off the search for prey after capturing one unit of prey i
J_i	year^{-1}	Asymptotic maximum consumption rate of predator i; within the bioenergetic and allometric framework it represents the realized maximum capacity of predator i to metabolize food, which is a fraction of its maximum physiological capacity to metabolize food ($a_{J_i} w_i^{-0.25}$)
f_{J_i}	Dimensionless	Fraction of its maximum physiological capacity to metabolize food realized by species i
a_{J_i}	year^{-1}·kg$^{0.25}$	Allometric coefficient of the maximum physiological capacity to metabolize food of species i; It depends on species i's metabolic type
ξ_{ij}	year^{-1}·tonne^{-1}	Multispecies Holling Type II functional response positive coefficient corresponding to the consumption of predator j of prey i
Q_j	tonne	Multispecies Holling Type II with predator interference functional response positive parameter corresponding to the baseline level of predator interference when predator j tends to zero
q_j	Dimensionless	Multispecies Holling Type II with predator interference functional response predator interference exponent; this parameter determines the degree of predator interference ($q_j = 0$ implies no predator interference, while $q_i \to \infty$ implies that predator interference precludes foraging)
γ_{ij}	year^{-1}·tonne$^{-b_j}$	Generalized Holling functional response positive coefficient corresponding to the consumption by predator j prey i
b_j	Dimensionless	Generalized Holling functional response shape parameter (exponent) corresponding to predator j
ρ_{ij}	year^{-1}·tonne^{-1}	Frequency-dependent predation functional response positive coefficient corresponding to the consumption by predator j of prey i
p_{ij}	Dimensionless	Frequency-dependent predation functional response positive coefficient corresponding to the preference of predator j for prey i
β_j	Dimensionless	Frequency-dependent predation functional response shape parameter (exponent) corresponding to predator j
τ_{ij}	year^{-1}·tonne^{-1}	Evans functional response positive coefficient corresponding to the consumption by predator j of prey i
δ_j	tonne^{-1}	Evans functional response shape parameter corresponding to predator j
a_{ij}	year^{-1}·tonne^{-1}	Ecosim functional response positive coefficient corresponding to the consumption by predator j of prey i; within the Ecosim framework it represents the rate of effective search for prey i by predator j
v_{ij}	year^{-1}	Ecosim functional response positive coefficient corresponding to the consumption by predator j of prey i; within the Ecosim framework it represents the rate at which unavailable prey i becomes available for predation by j
v_{ij}^c	year^{-1}	Ecosim functional response positive coefficient corresponding to the consumption by predator j of prey i; within the Ecosim framework it represents the rate at which available prey i becomes unavailable for predation by j

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Table B1 (*concluded*).

Symbol	Unit(s)	Description
$-\ln[\ell(\Theta)]$	Dimensionless	Minus loglikelihood
S_i^2	Dimensionless	Lognormal sample variance of the residuals of the species i biomass time series
B_{it}	tonne	Observed biomass of species i in year t
$\hat{B}_{it}$	tonne	Predicted biomass of species i in year t
AIC_c	Dimensionless	Akaike Information Criterion corrected for sample size
n_p	Dimensionless	Number of estimated parameters in a given model
N	Dimensionless	Total number of biomass estimates contained in the database
Δ_{AIC}	Dimensionless	Difference between the AIC_c of a given model and the AIC_c of the best ranked model (minimum AIC_c)
h_i	$year^{-1}$	Harvesting mortality (= fishing mortality) of species i
$\hat{\eta}_k(\Theta)$	Dimensionless	Importance function
$\eta(\Theta)$	Dimensionless	Posterior distribution
$w(\Theta)$	Dimensionless	Importance weight
$\ell(\Theta)$	Dimensionless	Likelihood
$\varphi(\Theta)$	Dimensionless	Prior distribution
$\hat{\eta}_k(\Theta)$	Dimensionless	Estimate of the posterior distribution $\eta(\Theta)$ obtained from the sample–importance–resample algorithm
θ_{MLE}	Variable	Generic representation of the maximum-likelihood estimator of a parameter
R_S	Dimensionless	Spearman's rank correlation coefficient
α_g	Dimensionless	Global significance level when multiple simultaneous comparisons are performed
α_c	Dimensionless	Significance level for each comparison when multiple simultaneous comparisons are performed
n_R	Dimensionless	Number of pairwise correlations performed among estimated parameters in a given model
B_{oi}	tonne	"Other prey" biomass available to predator i; this is a constant biomass for a given predator
t_0	year	Initial year
B_{i0}	tonne	Initial biomass for prey i

Note: The order of the symbols coarsely follows their order of appearance in the text.

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Evaluation of fish-injury mechanisms during exposure to turbulent shear flow

Zhiqun Deng, Gregory R. Guensch, Craig A. McKinstry, Robert P. Mueller, Dennis D. Dauble, and Marshall C. Richmond

Abstract: Understanding the factors that injure or kill turbine-passed fish is important to the operation and design of the turbines. Motion-tracking analysis was performed on high-speed, high-resolution digital videos of juvenile salmonids exposed to a laboratory-generated shear environment to isolate injury mechanisms. Hatchery-reared fall chinook salmon (*Oncorhynchus tshawytscha*, 93–128 mm in length) were introduced into a submerged, 6.35-cm-diameter water jet at velocities ranging from 12.2 to 19.8 m·s^{-1}, with a reference control group released at 3 m·s^{-1}. Injuries typical of turbine-passed fish were observed and recorded. Three-dimensional trajectories were generated for four locations on each fish released. Time series of velocity, acceleration, force, jerk, and bending angle were computed from the three-dimensional trajectories. The onset of minor, major, and fatal injuries occurred at nozzle velocities of 12.2, 13.7, and 16.8 m·s^{-1}, respectively. Opercle injuries occurred at 12.2 m·s^{-1} nozzle velocity, while eye injuries, bruising, and loss of equilibrium were common at velocities of 16.8 m·s^{-1} and above. Of the computed dynamic parameters, acceleration showed the strongest predictive power for eye and opercle injuries and overall injury level, and it may provide the best potential link between laboratory studies of fish injury, field studies designed to collect similar data in situ, and numerical modeling.

Résumé : La conception et la gestion des turbines requièrent une compréhension des facteurs qui blessent ou tuent les poissons qui les traversent. Nous avons fait une analyse du suivi du mouvement sur des bandes vidéo digitales à haute vitesse et haute résolution de jeunes salmonidés exposés à des environnements d'arrachement générés en laboratoire afin d'identifier les mécanismes vulnérants. Nous avons placé des saumons quinnat (*Oncorhynchus tshawytscha* de 93–128 mm de longueur) élevés en pisciculture dans un jet d'eau submergé de 6,35 cm de diamètre à des vitesses variant de 12,2–19,8 m·s^{-1}; le groupe témoin a été placé à une vitesse de 3 m·s^{-1}. Nous avons observé et noté des blessures caractéristiques de poissons qui ont traversé des turbines. Nous avons enregistré des trajectoires tridimensionnelles à quatre sites pour chaque poisson relâché, ce qui nous a permis de calculer des séries chronologiques de vitesse, d'accélération, de force, de secousse et d'angle de repli. Les blessures mineures, majeures et mortelles commencent à se manifester aux vitesses respectives de la lance d'eau de 12,2, 13,7 et 16,8 m·s^{-1}. Des blessures aux opercules se produisent aux vitesses de la lance de 12,2 m·s^{-1}, alors que les blessures aux yeux, les meurtrissures et la perte d'équilibre sont courantes aux vitesses égales et supérieures à 16,8 m·s^{-1}. Parmi les variables dynamiques calculées, l'accélération possède le pouvoir de prédiction le plus élevé pour les blessures aux yeux et aux opercules et pour le niveau global de blessures; elle fournit peut-être le meilleur lien potentiel entre les études des blessures des poissons en laboratoire, les études de terrain qui cherchent à obtenir des données semblables in situ et les modèles numériques.

[Traduit par la Rédaction]

Introduction

Despite advances in turbine design, dam operations, and juvenile fish bypass systems, turbine passage and spillway passage persist as sources of injury and mortality to downstream-migrating salmonids and other fish species in the Columbia River Basin (for overviews, see Coutant and Whitney 2000; Odeh and Sommers 2000; Čada 2001). Dam operators and design engineers are thus faced with the task of making these facilities safer for fish (i.e., more "fish-friendly"), as well as structurally and hydraulically sound and efficient for power generation. To design more fish-friendly facilities, engineers and biologists require reliable estimates of the hydrodynamic forces that fish can withstand.

Development of safer turbines and spillways is currently being approached in three general ways: (*i*) evaluating mortality and injury rates (biological response) in field studies utilizing passive integrated transponder (PIT) tags (CBFWA 1999) and radio-tracking, (*ii*) using laboratory studies to evaluate the physical stresses required to produce the biolog-

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Z. Deng,[1] C.A. McKinstry, R.P. Mueller, D.D. Dauble, and M.C. Richmond. Pacific Northwest National Laboratory, P.O. Box 999, Richland, WA 99352, USA.
G.R. Guensch. Balance Hydrologics, Inc., 841 Folger Avenue, Berkeley, CA 94710, USA.

[1]Corresponding author (e-mail: zhiqun.deng@pnl.gov).

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ical responses observed in the field studies, and (*iii*) using reduced-scale physical models and computational fluid dynamics (CFD) modeling techniques to assess design alternatives. Field studies involve tagging fish with radio and balloon tags, releasing them at various locations in the forebay of a dam or turbine intake, recovering them in the tailrace, and documenting their condition (e.g., Mathur et al. 1996, 2000) or using hydroacoustics (Skalski et al. 1996) to monitor passage and inferring passage efficiency (defined as the percentage of fish that pass by a dam by a means other than through the turbines). These types of studies, however, lack a way to determine the specific hydraulic conditions or physical stresses that the fish were exposed to, or the specific causes of the biological response. A promising means of measuring these hydraulic conditions in situ during downstream passage may be the concurrent release of the so-called sensor fish devices equipped to measure and record pressure and acceleration (Carlson and Duncan 2003; Deng et al. 2004). However, unless sensors are installed on the fish themselves, there is no direct way to quantify exactly what pressures, accelerations, or forces a given fish has sustained. One strategy for relating the sensor fish device measurements on the turbine environment to expectations of fish injury rates would be to develop correlation equations from laboratory studies.

Injuries and mortality of fish that pass through hydroelectric turbines can result from several mechanisms, such as rapid and extreme pressure changes, shear stress, turbulence, strike, cavitation, and grinding (Čada 2001). Laboratory studies provide a means of linking the observed biological responses to hydraulic conditions, forces, and stresses that are quantifiable and repeatable. Numerous laboratory studies conducted to date have made substantial progress in quantifying the levels of impact/strike (Turnpenny et al. 1992), shear (Turnpenny et al. 1992; Dauble et al. 2001; Neitzel et al. 2004), pressure (Turnpenny et al. 1992; Abernethy et al. 2001), cavitation (Turnpenny et al. 1992), and turbulence (Odeh et al. 2002) that certain fish can sustain. These data, in turn, have contributed to the development of a promising new generation of more advanced "fish-friendly" turbines, some of which are now being deployed. These advanced turbines typically have smaller gaps, wider leading edges, fewer blades, and redesigned stay vanes (Peltier 2003). Here we attempt to build on this body of data by characterizing the flow field of turbulent shear flows and the fish motion in sufficient detail to facilitate a more fundamental understanding of the mechanics of the injury process and the dynamic variables involved.

Motion tracking from video data is becoming a common experimental tool. Numerous researchers have used video data to study various aspects of swimming fish or their reactions (e.g., Hughes and Kelly 1996; Liao and Lauder 2000; Tang et al. 2000). However, these swimming studies typically do not require exceptionally high camera frame rates. High-speed (500–1000 frames·s^{-1}) video studies of fish tests, especially injury experiments, are less common. Some common high-speed applications of motion-tracking analysis include crash testing in the auto industry (Kang et al. 2001) and studies of impacts and projectile motion (e.g., Hrubes 2001; Tanaka et al. 2002).

The objective of this study was to use high-speed, high-resolution digital cameras and three-dimensional (3D) motion analysis to better quantify the kinematic and dynamic parameters associated with the exposure of fish to turbulent shear flow. The kinematic parameters included the velocity (v), acceleration (a), jerk (J), and bending angle (θ_b) of the fish, while the dynamic parameter was the bulk force (F) on the fish. The injury type and severity were related to fish size (length and mass), exposure strain rate, and magnitude of kinematic and dynamic parameters computed from video-derived 3D trajectory paths.

Methods

Test fish

We tested subyearling fall chinook salmon (*Oncorhynchus tshawytscha*) from stocks originating at the Priest Rapids Hatchery in Washington State in mid- to late September 2003. The test fish were around 7 months old and ranged from 93 to 128 mm in length and from 8.1 to 23.5 g in mass. All test fish were in good to excellent condition prior to testing, in presmolt stage, and actively migrating.

Test facility

A rectangular flume containing a submerged water jet was used to create a quantifiable shear environment consistent with conditions expected within a hydroelectric turbine. The flume was 9 m long, 1.2 m wide, and 1.2 m deep when filled with water. A conical stainless-steel nozzle was bolted to a flange inside the flume at one end. The nozzle began at a diameter of 25.4 cm, constricted to a 6.35-cm diameter over a length of 50.8 cm, and terminated through a tube 4.5 cm long and 6.35 cm in diameter (Fig. 1). A flow conditioner was incorporated upstream of the nozzle to reduce inlet turbulence. Nozzle velocities in excess of 20 m·s^{-1} were achievable with a centrifugal pump with a programmable electronic speed controller.

Fish were actively introduced into the jet through a polycarbonate introduction tube (60 cm long × 3.18 cm in diameter) with a 0.81 m·s^{-1} velocity. The tube was fastened above the nozzle at an angle of 30° (Fig. 1). The terminus of the introduction tube was positioned above and in front of the terminus of the nozzle, with only a 1-cm vertical gap to ensure that test fish contacted the jet. The introduction flow was necessary to ensure that fish passed the terminus of the introduction tube smoothly. Fish were exposed to the following water jet velocities: 3.0 (reference control), 12.2, 13.7, 15.2, 16.8, 18.3, and 19.8 m·s^{-1}.

Fish exposures to the water jet were digitally recorded through viewing windows located on the side and bottom of the flume. The velocity field was characterized using a laser Doppler velocimeter. Neitzel et al. (2000, 2004) contains more detailed information on tank/pump specifications and velocity and turbulence characterization.

Fish handling

To re-identify individual fish during the post-test monitoring, each fish was fitted with a PIT tag prior to testing. The PIT tags (AVID/Destron-Fearing TX1400ST, 12 mm long, 134.2 kHz; Biomark Inc., Boise, ID 83714) were inserted following the protocols outlined in the PIT Tag Mark-

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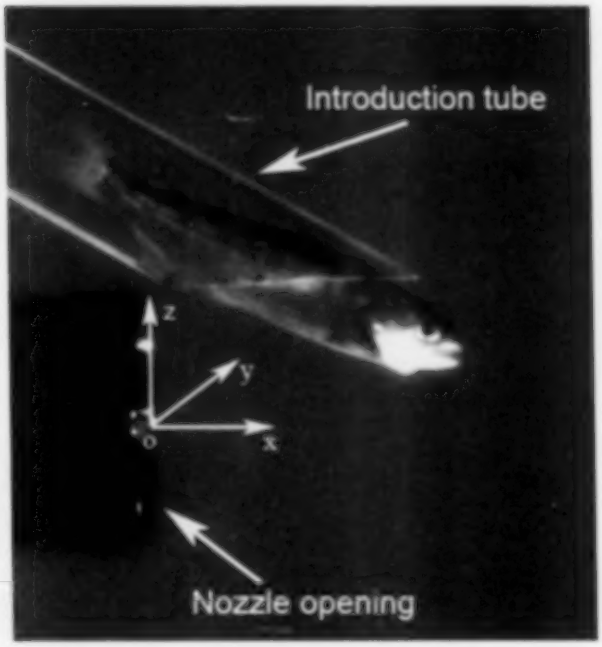
Fig. 1. Nozzle, introduction tube, coordinate system, and a test fish being released. Note that the *y* axis is essentially directed into the page.



ing Procedures Manual (CBFWA 1999). Fish were anesthetized in 40 mg·L^{-1} MS-222 (3-aminobenzoic acid ethyl ester) solution in a water bath held to a constant temperature (14 °C). Immediately after being tagged, each fish was weighed and measured and its tag was read with a portable Destron-Fearing 2001F PIT tag reader. Fish were allowed a 5-day recovery period before being tested.

Test fish were held near the test facility at low densities in a 1700-L trough with a high water turnover rate. The test flume and holding trough were supplied with 16–17 °C well water. For each test, a fish was randomly captured from the holding trough using a small dip net and scanned with the portable PIT tag transceiver. The unique PIT tag code was recorded and then the fish was placed into a section of clear tubing (cartridge) containing a small volume of water. Each fish was then transferred to the introduction tube, held in the tube until the jet stabilized, and then introduced into the flow field of the jet with the injection flow. The duration of the injection was about 1 s, and the entire deployment and exposure process took less than 20 s.

Within about 10 s following each individual exposure, the pump was turned off and fish were captured from the flume with dip nets. Swimming impairments such as loss of equilibrium, lethargy, and disorientation were evaluated based on the swimming behavior during recapture.

Injury characterization

After recapture, each fish was examined to assess the type and severity of the external injuries (i.e., biological responses) sustained and the direct mortality (immediate and delayed). Following injury evaluation, the fish were photographed and placed in small cages located in the holding trough. Each test group (including reference control fish) was held for 96 h to monitor delayed mortality or other effects indicative of stress or injury (e.g., dark discoloration, lethargy, loss of equilibrium, fungal/disease infection, and osmoregulation problems).

Injury categories included eye damage, descaling, gill/operculum damage, isthmus damage, split fins, bruising/discoloration, and spinal fracture. Disorientation and loss of equilibrium, characterized by reduced swimming ability, were also considered indicators of potentially severe injury and impairment. All these injuries are externally visible injuries and may or may not be indicative of other injuries.

Injury levels similar to those used in Neitzel et al. (2000, 2004) were assigned values from 0 to 4 according to the following criteria: (0) no injury, no observable physical injury or brief minor disorientation; (1) single minor injury, visible but not life-threatening injuries, such as minor bruising, operculum damage, slight gill bleeding, minor isthmus tear, minor descaling, or temporary disorientation; (2) multiple minor injuries, more than one minor injuries but not life threatening; (3) major injury, life-threatening injuries such as severe bruising, bleeding, tearing, creasing, multiple injuries, or prolonged swimming impairment, disorientation, and loss of equilibrium; and (4) mortality, immediate or delayed mortality.

These injury-level and injury-type data were recorded for each fish released and were compiled into a table with the fish information and the dynamic parameter values.

Video recording and processing

Video images of exposed fish were captured using two identical high-speed digital cameras (Photron PCI FastCAM 1280; Photron USA, Inc., San Diego, Calif.) equipped with 50-mm lenses. The cameras captured side (*X*–*Y* plane) and bottom (*X*–*Z* plane) views through polycarbonate viewing windows in the side and bottom of the tank. Halogen lamps were used to provide the desired illumination and a gray-colored back panel was used to provide optimal contrast. The cameras recorded fish orientation and location from the moment a fish descended the introduction tube and contacted the shear environment until it was swept out of the immediate shear environment (~0.5 m) downstream. An entire exposure sequence lasted only a fraction of a second. The two cameras recorded each event simultaneously at 1000 frames·s^{-1}. Cameras were focused using a high-contrast resolution target positioned along the axis of the nozzle. Calibration of the field of view for fish metrics was accomplished by using the outer diameter of the nozzle.

The trajectories of four separate points on each fish (nose, head, centroid, and tail) were manually tracked frame by frame in a motion-tracking software package (Visual Fusion® 4.2; Dr. Jack Sanders-Reed, Boeing-SVS Inc., Albuquerque, New Mexico). The side and bottom view tracks were then combined to form a 3D trajectory from which time series of the velocity, acceleration, jerk, bending, and force magnitudes were calculated. These higher-order variables were computed from data smoothed using a 5-point boxcar average. Finally, the average and peak values of each variable were computed for each time series and used in the analysis.

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Table 1. Summary of the sample characteristics for each nozzle velocity, where U, L, m, and IL denote the nozzle velocity, length, mass, and injury level, respectively.

Nozzle velocity, U (m·s^{-1})	Mean fish length, $\bar{L}$ (mm)	Fish length variance, σ_L (mm)	Mean fish mass, $\bar{m}$ (g)	Fish mass variance, σ_m (g)	Mean injury level, $\bar{IL}$[a]	Injury level variance, σ_{IL}[a]
3.0	112.9	8.69	16.5	3.67	0.1	0.30
12.2	111.4	6.31	15.8	3.65	0.43	0.60
13.7	107.0	9.15	14.0	4.13	1	0.72
15.2	113.0	8.24	15.9	3.67	1.24	0.46
16.8	111.2	7.30	15.4	3.31	1.73	0.57
18.3	108.0	7.79	14.1	3.29	2.36	0.57
19.8	112.2	7.00	15.5	3.38	2.24	0.78

[a]Unitless.

Data analysis

Kinematic and dynamic parameters

The kinematic and dynamic parameter time series were computed from the change in the x, y, z position of the centroid of the fish for each successive time step (Fig. 1). Only random errors associated with motion analysis were considered based on the assumption that the systematic errors were relatively small in comparison. To reduce random errors, the position data were smoothed with a simple 5-point running average prior to the computation of higher-order parameters. Given an assumed maximum random error of one pixel in each direction associated with the motion analysis methodology, the related random errors for other parameters were then estimated. The errors for velocity (v), acceleration (a), jerk (J), and force (F) are 0.253 m·s^{-1}, 50.6 m·s^{-2}, 10120 m·s^{-3}, and 0.759 N, respectively. Simplified expressions for each variable are shown in eqs. 1–5 below.

$$(1) \qquad v = \begin{pmatrix} dx/dt \\ dy/dt \\ dz/dt \end{pmatrix}$$

$$(2) \qquad a = dv/dt$$

$$(3) \qquad J = da/dt$$

$$(4) \qquad F = m \cdot a$$

$$(5) \qquad \theta_b = \arccos\left(\frac{A^2 + B^2 - C^2}{2AB}\right)$$

where m is the fish mass, dt is the time step (equal to the time between digitized frames, 0.001 s), and changes in variables between successive digitized frames are indicated by the differential (d). For example, $dx = x_i - x_{i-1}$, where i indicates the frame number. The values A, B, and C are the three sides of a triangle formed by the bent fish, where A and B are the sides formed by the fish body and C is the side connecting the head and tail (opposite to θ_b). The peak value of each dynamic parameter for each release was used in the subsequent statistical analysis.

Statistical analysis

The five-level scale classifications of observed fish injuries were used to define binomial response variables for different levels and types of injury. Binary injury responses were fit to the set of peak dynamic parameters in separate logistic regression models of the form shown in eq. 6.

$$(6) \qquad p(x) = \frac{e^{\mathbf{X}\boldsymbol{\beta}}}{1 + e^{\mathbf{X}\boldsymbol{\beta}}}$$

where $p(x)$ is the expected probability of a fish sustaining a specified level or type of injury, $\boldsymbol{\beta}$ is the vector of fitted coefficients, and $\mathbf{X}$ is the model matrix. Confidence intervals at the 95% level were computed as well.

Model selection was performed using a sequential analysis of deviance approach (McCullagh and Nelder 1989) to arrive at the most parsimonious set of kinematic and dynamic parameters in the final model. Individual parameters were entered into the model in descending order of deviance as computed from a univariate logistic regression of each parameter on the binary response. Since overdispersion was evident in the data, the more conservative F test was used at each model-building step to assess model improvement and account for lack of fit.

Using logistic regression in this way, a functional relationship was established between the expected biological injury rate and a subset of the most predictive kinematic and dynamic parameters. Binary responses were defined for minor or worse injury, major or worse injury, eye damage, and operculum damage.

Results

Biological response

Twenty-one fish were released headfirst at each nozzle velocity (3.0, 12.2, 13.7, 15.2, 16.8, 18.3, and 19.8 m·s^{-1}). The basic characteristics of each group (summarized in Table 1) show that the groups did not differ significantly in mass or length. They also show that the mean injury level for each group increased with increasing nozzle velocity up to 18.3 m·s^{-1} and then decreased slightly at 19.8 m·s^{-1}. This decrease was within the uncertainty range of the data as estimated by the sample standard deviations.

Minor injuries occurred at the lowest nozzle velocity, 12.2 m·s^{-1}, and in two reference control fish. Appreciable levels (38%) of major injury occurred at 13.7 m·s^{-1}. Substantial total mortality (14%) occurred at 16.8 m·s^{-1} (Fig. 2). Mortality within 1 h following exposure was first observed at 16.8 m·s^{-1} and increased to nearly half of the fish tested at 18.3 and 19.8 m·s^{-1}. Fewer additional mortalities occurred at

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Fig. 2. Summary of injury levels at each nozzle velocity (n = 21 for all nozzle velocities). Minor injury, hatched bars; major injury, stippled bars; 1-h mortality, open bars; 24-h mortality, shaded bars; total mortality, solid bars.

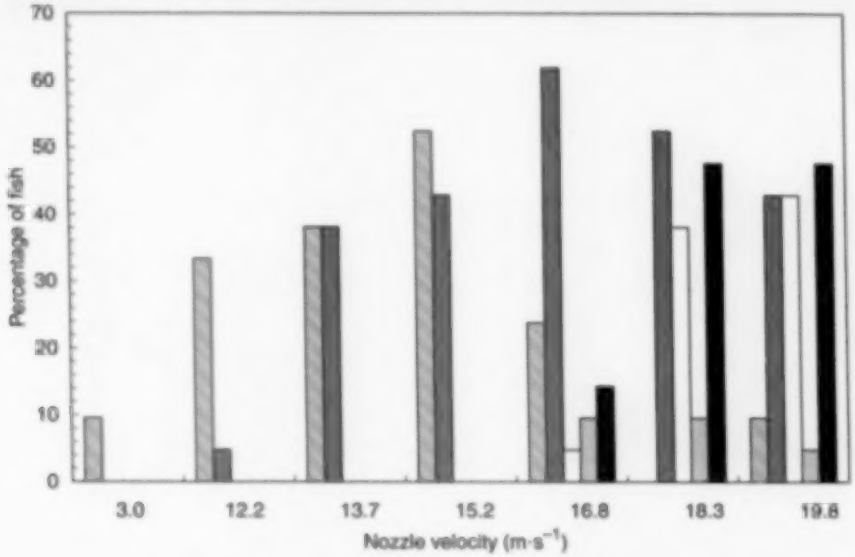

Fig. 3. Example of inverted opercle from fish released at 19.8 m·s^{-1}.

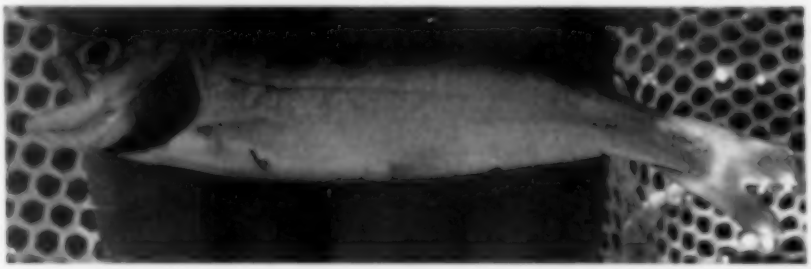

Table 2. Pairwise correlation between nozzle velocity, acceleration, and jerk of fish and force sustained by fish.

Velocity			
0.829	Acceleration		
0.695	0.876	Force	
0.817	0.843	0.741	Jerk

24 h and none occurred at 96 h (Fig. 2). Injuries to the operculum (Fig. 3) occurred in 70%–90% of the fish tested at nozzle velocities of 15.2 m·s^{-1} or greater, making the operculum the most commonly injured organ. Eye damage, bruising, and loss of equilibrium occurred in 40%–50% of the fish released at nozzle velocities of 16.8 m·s^{-1} and above (Fig. 4).

Motion analysis results

Motion analysis results computed from the fish tracks for three nozzle velocities, 3 m·s^{-1} (reference control), 13.7 m·s^{-1} (low speed), and 18.3 m·s^{-1} (high speed), show the general pattern of each parameter (Fig. 5). At the point of entrainment into the jet, the three groups differ substantially, with the exception of downstream distance (x) for the low- and high-speed releases (Fig. 5*a*). Generally, the high-speed release sustained the most severe exposure to all the parameters and the reference control fish experienced the least (Figs. 5*b*–5*f*). Estimates of jerk were very high for the non-control groups, especially for the high-speed release group, and very sensitive to changes in acceleration (Fig. 5*d*). The net force on the body of the fish differs from the acceleration by a constant factor, the fish mass (Figs. 5*c* and 5*e*). Bending angle, the interior angle of the fish as it exited the tube (e.g., 180° means the fish is straight and 0° means the fish is folded in half), was most severe at 40° for the fish released at a high nozzle velocity (Fig. 5*f*).

Statistical analysis results

Pairwise correlations showed high levels of positive correlation between nearly all the variables (Table 2). This was largely because all kinematic and dynamic parameters were computed from the same video-derived frame-to-frame displacements. Force and velocity were least correlated, whereas force and acceleration, as expected, were most correlated.

The high degree of correlation between the kinematic and dynamic parameters (Table 3) preclude incorporation of

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Fig. 4. Summary of different injury types at each nozzle velocity (n = 21 for each nozzle velocity). Eye damage/loss, solid bars; opercle damage, open bars; bruised, shaded bars; loss equilibrium/lethargy, hatched bars.

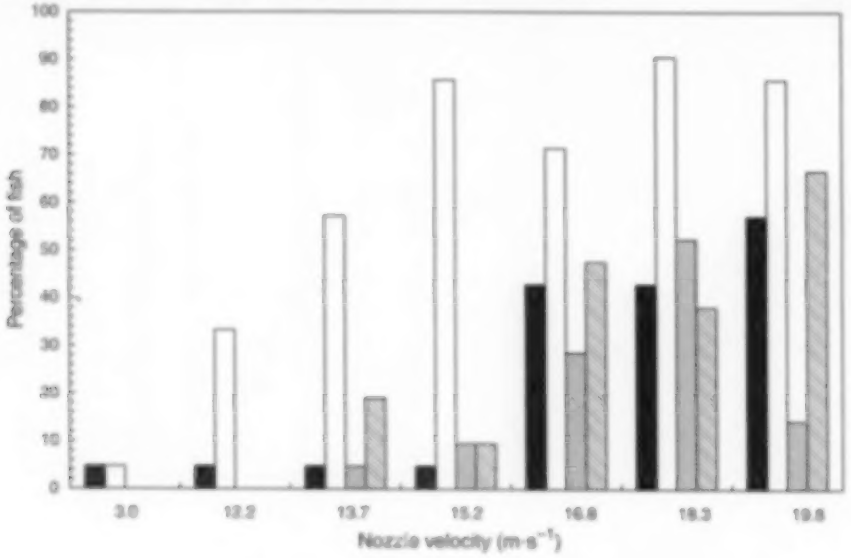

Table 3. Univariate modeling correlations between incidence of injury and kinematic and dynamic parameters from logistic regression of individual fish injury levels.

	df	Deviance	Residual df	Residual deviance	F value	Pr(F)
Velocity	1	67.38	143	99.43	73.16	<0.001
Acceleration	1	74.56	143	92.25	85.87	<0.001
Force	1	59.21	143	107.60	43.75	<0.001
Jerk	1	59.09	143	107.72	46.80	<0.001

Table 4. Analysis of deviance ordered by univariate model results from logistic regression of individual fish injury levels.

	df	Deviance	Residual df	Residual deviance	F value	Pr(F)
Null			144	166.81		
Acceleration	1	74.56	143	92.25	87.38	<0.001
Velocity	1	2.26	142	89.99	2.64	0.106
Force	1	0.00	141	89.99	0.00	0.988
Jerk	1	0.21	140	89.78	0.25	0.618

more that just acceleration into the binomial model. Sequential construction of the model in this fashion controls for these high correlations between candidate model predictor variables (Table 4). Because acceleration showed the highest predictive power of the binary injury variables, it was entered first into the model, followed by velocity, force, and jerk. However, none of the additional variables showed significant improvement in model fit over the model containing acceleration.

The results of the binomial logistic regression relate the probability of specific biological responses to acceleration (Fig. 6). The probability of minor injury or worse increased quickly starting at 100 m·s^{-2} and reaching nearly 1.0 by 900 m·s^{-2} (Fig. 6*a*). The probability of major injuries was similarly shaped to that for minor injuries but was increased by roughly 200 m·s^{-2} towards higher accelerations (Fig. 6*b*). The expected probabilities of an eye (Fig. 6*c*) or operculum (Fig. 6*d*) injury were similar and increased slowly at low acceleration levels and became linear beyond 700 m·s^{-2} (Figs. 6*c* and 6*d*).

Discussion

Thresholds of injury

The onset of injury or biological response at or above the 10% level was used to indicate threshold levels of parameters evaluated in this study. Our tests showed the onset of minor, major, and fatal injuries to occur at nozzle velocities of 12.2, 13.7, and 16.8 m·s^{-1}, respectively. Injuries associated with the operculum were most common at all nozzle velocities and were the only injuries to occur at significant levels at the lowest test jet velocity of 12.2 m·s^{-1}. Loss of

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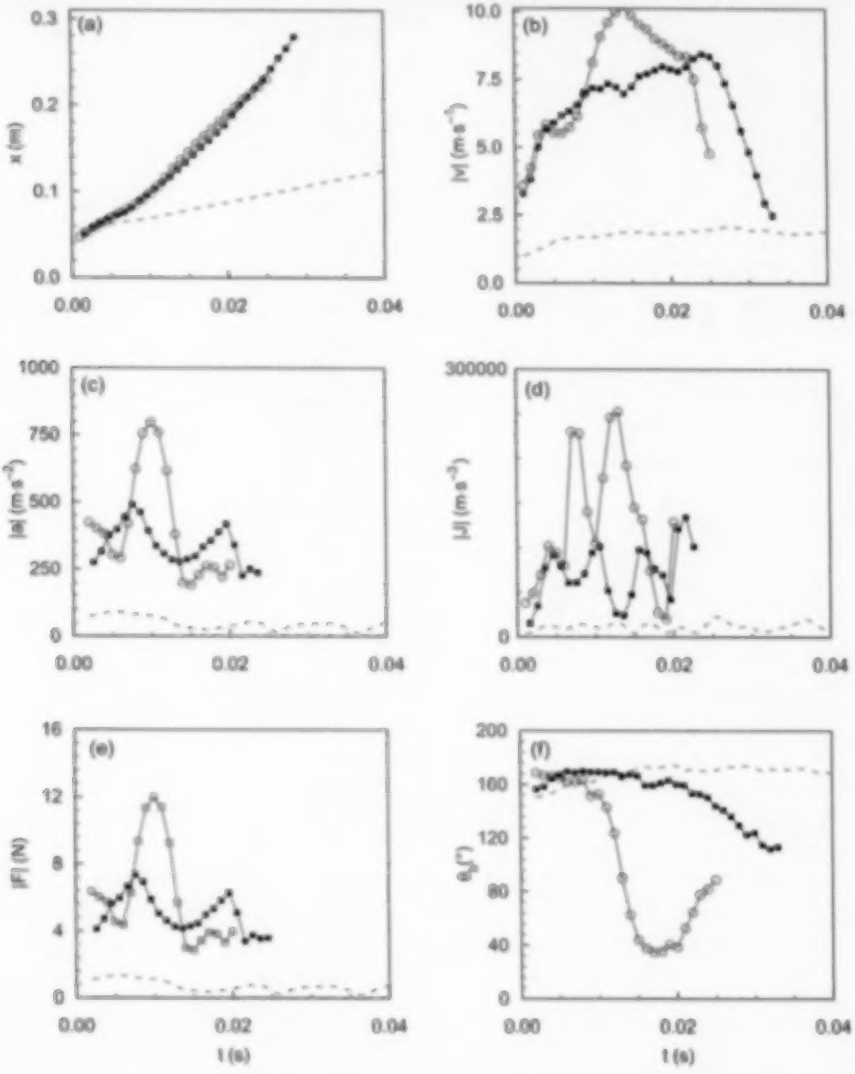
Fig. 5. Examples of motion analysis results of fish releases at three nozzle velocities (only one out of 21 releases per nozzle velocity is plotted) for the bulk kinematic/dynamic parameters: (*a*) streamwise location (x); (*b*) velocity (v); (*c*) acceleration (a); (*d*) jerk (J); (*e*) force (F); (*f*) bending angle (θ_b). Velocities: 3 m·s^{-1}, broken line; 13.7 m·s^{-1}, solid squares; 18.3 m·s^{-1}, open circles.



equilibrium occurred in more than 10% of fish, at the next highest nozzle velocity of 13.7 m·s^{-1}, although it decreased to 9% at 15.2 m·s^{-1}. Eye damage, bruising, and loss of equilibrium all became clearly prevalent at 16.8 m·s^{-1}.

These results can be compared, either directly or through simple conversions, to those reported by other investigators. Neitzel et al. (2000, 2004) conducted similar tests and expressed the jet severity in terms of exposure strain rate (s^{-1}), which was essentially the fluid strain rate computed at the scale of a test fish (i.e., jet velocity/approximate width of a test fish). Converting our critical jet velocities in this manner gives key exposure strain rates of 677, 761, and 933 s^{-1} for minor, major, and fatal injuries, respectively. Our exposure strain rate value of 677 s^{-1} for the onset of minor injuries corresponds well to the 683 s^{-1} value documented by Neitzel et al. (2000, 2004). Turnpenny et al. (1992) also conducted similar experiments and noted the onset of severe eye and operculum injuries to occur at a shear stress level of 1920 N·m^{-2}, which corresponds to a jet velocity of 15 m·s^{-1} and an exposure strain rate of ~833 s^{-1}, which is within range of our results.

In contrast to jet velocity and exposure strain, which basically represent flow-field characteristics, the kinematic and dynamic parameters determined from motion tracking were specific to each individual fish. Of these parameters, acceleration of the fish correlated most strongly with fish injury. Threshold or critical levels of fish acceleration were also determined based on the probability of injury as a continuous function of the acceleration of the fish. For example, the 0.1, or 10%, probability of minor, major, eye, and operculum in-

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Fig. 6. Fitted probability of four types of injury as a function of acceleration, with 95% predictive confidence intervals (broken lines), as derived from binary logistic regression: (*a*) minor; (*b*) major; (*c*) eye; (*d*) operculum.

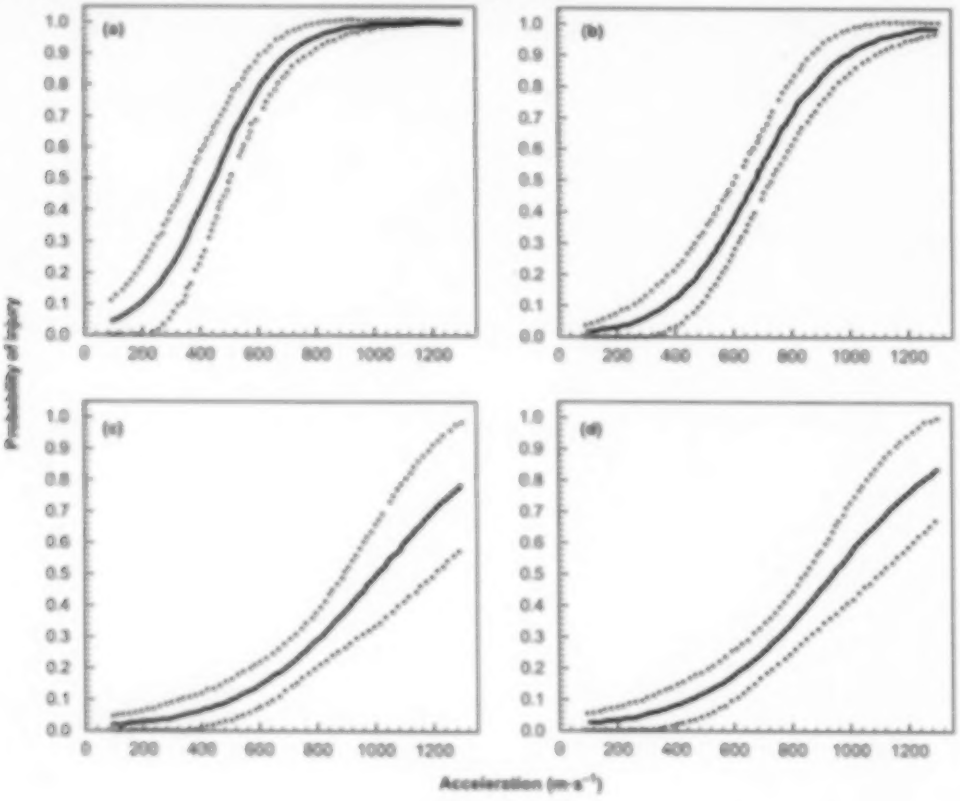

Table 5. Accelerations ($m \cdot s^{-2}$) of fish corresponding to injury probabilities of 5%, 10%, and 15% with 95% confidence intervals in parenthesis.[a]

Injury type	5% ($P = 0.05$)	10% ($P = 0.10$)	15% ($P = 0.15$)
Minor injury	100 (0–280)	180 (20–310)	240 (140–350)
Major injury	240 (90–380)	340 (210–440)	360 (250–460)
Eye	300 (80–520)	500 (310–640)	600 (360–710)
Opercle	250 (90–490)	440 (270–600)	550 (390–670)

[a]For example, 10% probability of major injuries corresponds to fish acceleration level of 340 $m \cdot s^{-2}$, with the lower and upper curves bounding the 95% confidence interval being 210 $m \cdot s^{-2}$ and 440 $m \cdot s^{-2}$, respectively.

juries corresponds to fish acceleration levels of 180, 340, 500, and 440 $m \cdot s^{-2}$, respectively. Ranges for these estimates were determined based on the lower and upper curves bounding the 95% confidence interval (Table 5).

The relationships described here between fish injury and either exposure strain rate or acceleration will be most effectively used in combination with information on what passing fish are actually exposed to. Particle tracking algorithms within CFD models (Richmond et al. 2004) or accelerations measured in the field with a sensor fish (Carlson and Duncan 2003) are two possible sources of exposure information. For example, one could use the relationships presented here to estimate probability of injury from CFD-derived estimates of the exposure strain rate or the acceleration to which particles are exposed, greatly enhancing the potential to use CFD as a biohydraulic design tool. Similarly, the acceleration time series measured in the field with the sensor fish device (Carlson and Duncan 2003) could be converted to a time series of fish injury probability using the probability of injury versus fish acceleration relationship, which would enhance the effectiveness of the sensor fish device as an assessment tool. These new and innovative approaches will gradually come to fruition over the next few years as CFD modeling capabilities improve and the sensor fish device is refined.

Mechanics of injury

The vulnerability of fish to injury in turbulent shear flows is best understood in terms of fish physiology and the resulting stresses on the fish. Salmonids are evolutionarily adapted

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for swimming head-on into the flow. In this orientation, they are streamlined to minimize drag, can tolerate extremely severe velocities, velocity changes, or accelerations, and can even use shear stresses and turbulence to their advantage (Vogel 1996; Liao et al. 2003). They are poorly adapted, however, to flow coming from behind. Such reverse flows can lift and tear off scales, pry open the operculum, rupture or dislodge eyes, and damage gills.

The opercula are most vulnerable to damage from reverse flow, as observed here, because they are easily pried open and then flare out and act as a parachute or spinnaker, essentially capturing the energy contained in a disproportionately large area of flow. This parachute effect increases drag and accelerates the fish faster than if it were oriented head-on to the flow field. Most importantly, however, the anatomical shape and structure is such that the stress is focused on the two small attachment points of each operculum—the upper left and right attachment points on the head, and the shared lower attachment point at the isthmus. A pushing or pressure force applied to the entire operculum is transmitted to the fish as a tensile stress focused at these pin-sized attachment points, in a manner somewhat analogous to tearing a partially torn piece of paper or breaking a v-notched shaft.

Value of kinematic and dynamic approaches in a hydraulic environment

Our study suggests that fish injuries were proportional to the velocity of flow field and also subject to stochastic factors acting in combination, such as the orientation of the body and vulnerable anatomy of the fish when it encounters the water jet, the reaction of the fish, and the characteristics of the water jet at the instant of contact. The stochastic component is evidenced by the slightly reduced average injury level for the group released at the highest nozzle velocity (e.g., 19.8 $m \cdot s^{-1}$), an observation for which there was no other defensible explanation, and the large standard deviation in injury levels for each jet velocity. This stochasticity can make simple relationships between flow field characteristics, such as velocity and shear, and biological response misleading. The use of kinematic and dynamic parameters overcomes this problem because they describe the actual motion of each individual fish and, therefore, more effectively account for the stochastic variations. When incorporated into an empirical modeling approach, as shown here, these kinematic and dynamic parameters are more robust predictors of fish injury. Further, these kinematic and dynamic parameters are more suitable for comparison with sensor fish data and CFD particle-tracker output.

The approach described here to estimate the bulk kinematic motion and mechanical force sustained by a fish in a hydraulic environment is also more applicable to turbine passage than measuring forces and stresses directly and then attempting to translate them to a hydraulic environment. More accurate measures of the forces on specific organs would be possible using direct mechanical means (e.g., Geerlink and Videler 1987; Long 1992; Miller 2001) instead of the in situ method used here. Direct forces, however, would be difficult to apply in a manner relevant to what a fish experiences in a hydraulic environment. Also, precise mechanical measures of localized yield strength of specific parts of individual organs such as operculum or eyes may not be useful to turbine designers at the present time, because such fine-scale phenomena are not typically available from CFD turbine models used in design or field studies. Currently, the best method of assessing fluid-induced forces is to measure them in the fluid environment as shown here or, alternatively, by using force measurement tools such as tensiometers and force transducers. Forces and stresses measured this way can be related to information incorporated into models used in turbine design, such as velocity distributions, strain rates, shear stresses, turbulence, and possibly particle acceleration if used with a particle-tracking routine.

In summary, a number of basic conclusions can be drawn from this study. The onset of minor, major, and fatal injuries occurred at 12.2, 13.7, and 16.8 $m \cdot s^{-1}$ jet velocities, respectively. These jet velocities correspond to exposure strain rates of 677, 761, and 933 s^{-1}, which agree with previous experiments. Motion-tracking analysis provides a means of measuring the bulk kinematics, forces, and deformations sustained by fish in experimental hydraulic environments. The kinematic and dynamic parameters that can be computed from the motion-tracking data (v, a, F, J, and θ_b) incorporate some of the inherent stochasticity of the fish releases and, therefore, can be more rigorously related to biological response than parameters based solely on simple jet characteristics. The bulk acceleration of the fish was most predictive of all injury types and overall injury level. The predictive power of force would probably be stronger if a broader range of fish body masses were tested. Acceleration is a more convenient parameter than force in some respects because it can be compared directly with both CFD output and field-derived sensor fish data.

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Ecotypic differentiation of native rainbow trout (*Oncorhynchus mykiss*) populations from British Columbia

E.R. Keeley, E.A. Parkinson, and E.B. Taylor

Abstract: We sampled 34 native rainbow trout (*Oncorhynchus mykiss*) populations over a wide geographic area of British Columbia to determine whether variation in morphology is related to differences in habitat or fish community characteristics experienced by a population. After correcting for differences in body size, the most dramatic differences occurred in external characteristics between stream- and lake-dwelling populations. Rainbow trout from streams had more robust bodies with larger caudal peduncles and heads and longer paired fins than rainbow trout from lakes. Unlike other lake populations, piscivorous rainbow trout populations had relatively large heads and mouths that were more similar in size to those of stream-dwelling populations. We found fewer differences in the size of internal organs across ecotypes, producing little predictive ability of these characteristics to differentiate populations of rainbow trout. We also sampled 27 additional rainbow trout populations with unknown fish communities to determine how well large-scale patterns predict morphological differentiation over a smaller spatial scale. Of the five ecotypes that we detected at a smaller scale, the largest differences again occurred between stream and lake populations. Our data suggest that external morphological variation among populations of rainbow trout covaries with ecological conditions at a variety of spatial scales, particularly between lakes and rivers.

Résumé : Nous avons échantillonné 34 populations indigènes de truites arc-en-ciel (*Oncorhynchus mykiss*) dans une grande région géographique de la Colombie-Britannique afin de déterminer si la variation morphologique est reliée à des différences d'habitat ou des caractéristiques des communautés de poissons rencontrées par la population. Après correction pour les différences de taille, les différences les plus spectaculaires existent entre les caractéristiques externes des populations des cours d'eau et celles des lacs. Les truites arc-en-ciel des cours d'eau ont un corps plus robuste avec un pédoncule caudal et une tête plus grands et de plus longues nageoires paires que les truites des lacs. Contrairement aux autres populations des lacs, les truites arc-en-ciel piscivores ont une tête et une bouche relativement plus grandes, de taille plus semblable à celles des populations habitant les cours d'eau. Il existe moins de différences entre les écotypes en ce qui concerne la taille des organes internes et ces caractéristiques n'ont qu'un faible pouvoir de prédiction pour distinguer les populations de truites arc-en-ciel. Nous avons aussi échantillonné 27 populations additionnelles de truites arc-en-ciel appartenant à des communautés de poissons inconnues afin de vérifier dans quelle mesure les patterns à grande échelle permettent de prédire la différentiation morphologique sur une échelle spatiale réduite. Des cinq écotypes reconnus à plus petite échelle, les différences les plus accentuées se produisent encore entre les populations des cours d'eau et celles des lacs. Nos données laissent croire que la variation morphologique externe de la truite arc-en-ciel est en covariation avec les conditions écologiques à plusieurs échelles spatiales, particulièrement entre les lacs et les rivières.

[Traduit par la Rédaction]

Introduction

Intraspecific variation in phenotypic traits has been repeatedly demonstrated among populations in a variety of plant and animal species, and much of this variability appears to represent adaptation to local conditions (Sultan 1995; Smith and Skùlason 1996). Turesson (1922) was the first to coin the term "ecotype" to describe geographical isolates of plants that were consistently associated with particular environmental or habitat characteristics as a result of selection in those environments (e.g., alpine ecotype). Such variability has not only been an essential component of stud-

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E.R. Keeley.[1] Department of Biological Sciences, Box 8007, Idaho State University, Pocatello, ID 83209, USA.
E.A. Parkinson. British Columbia Ministry of Water, Land and Air Protection, 2204 Main Mall, The University of British Columbia, Vancouver, BC V6T 1Z4, Canada.
E.B. Taylor. Department of Zoology, Biodiversity Research Centre, and Native Fishes Research Group, The University of British Columbia, 6270 University Boulevard, Vancouver, BC V6T 1Z4, Canada.

[1]Corresponding author (e-mail: keelerne@isu.edu).

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ies of the evolutionary origin of geographic variation (Mayr 1963; Gould and Johnston 1972) but is also increasingly viewed as essential in biodiversity conservation (e.g., Crandall et al. 2000). Effective conservation strategies need to maintain this diversity to ensure that the full evolutionary potential of a species is protected, especially as a buffer against extinction in the face of environmental change (Scudder 1989; Fraser 2000). Empirical mapping of this information for every population of every species is, however, clearly impossible. In this paper, we explore a method of predicting patterns of potentially adaptive variation among populations of rainbow trout (*Oncorhynchus mykiss*) using a variety of existing information for north-temperate salmonid fishes. We then test this methodology by measuring a series of morphological traits of rainbow trout from native populations over a wide geographic area. Our second objective is use these data to draw some general conclusions concerning the patterns of adaptive radiation that might be expected to occur among isolated populations of freshwater fish.

Our predictions of patterns of morphological variation are based on three types of information. First, breeding studies have established the genetic basis for a variety of phenotypic traits in both rainbow trout and closely related species. Second, correlations between phenotypic traits and habitat variation, among both species and populations of freshwater fishes, suggest that many of these traits are adaptive (Robinson and Parsons 2002). Finally, our ability to extend our predictions to the entire species range depends on large, integrated databases that contain a variety of physical, chemical, and biological information about individual water bodies. Our data set is an extension of previous studies that have focused on detailed comparisons of a limited number of populations or variation in a few traits over many populations (Schluter and McPhail 1993; Taylor 1999).

If ecological conditions experienced by different populations of rainbow trout are important in selecting for phenotypic characteristics, our most general prediction was that morphological variation would not be randomly associated with environmental variation, but rather, it would be consistently correlated with variation in habitat or community structure. Specifically, we made a number of predictions related to three general areas of ecological morphology that have been used to infer adaptation in other systems: feeding, locomotion, and organ size. Although distinct ecotypes have been documented in a number of northern fish taxa (Robinson and Wilson 1994; Taylor 1999), diversity appears to be especially high in salmonids (Taylor 1991, 1999). In particular, rainbow trout in British Columbia are a good model species for our study because of their diverse suite of life histories, multiple phylogenetic groups with distinct evolutionary histories, and diversity of habitats and communities in which they are found (Taylor and Haas 1996; McCusker et al. 2000).

Morphological adaptations associated with feeding specialization appear to be common in north-temperate freshwater fish, including the salmonids. In comparisons among species and populations, larger diet items are associated with shorter and more widely spaced gill rakers, larger mouths, and larger heads. These types of differences have been repeatedly demonstrated among planktivore, insectivore, and piscivore diet specialists. Piscivores have large mouths for a given body size in comparison with nonpiscivorous species (Wainwright and Richard 1995). Among lake populations, the presence of benthic competitors such as catostomid fish appears to cause brook trout (*Salvelinus fontinalis*) to shift to a planktivorous diet with a feeding morphology of more narrowly spaced gill rakers (Magnan 1988). In contrast, the presence of plankton-feeding specialists has been associated with shifts by sympatric species to a more benthically oriented diet and with a change to shorter, more widely spaced gill rakers (Lindsey 1981). If the presence or absence of either type of competitor has a significant influence on shaping rainbow trout phenotypes, then this too should be reflected in their morphological characteristics.

Morphological characteristics associated with swimming ability are also thought to be influenced by different habitat conditions. For instance, salmonids that live in fast-flowing stream habitats tend to have longer fins and a more robust body than slow-flowing stream or lake-inhabiting populations (Swain and Holtby 1989; Pakkasmaa and Piironen 2001; Imre et al. 2002). The genetic basis for such variation has been verified in at least some salmonids (e.g., Riddell et al. 1981; Taylor and McPhail 1985).

Variation in habitat characteristics may also be related to the relative size of internal organs. Although we know of no similar comparison for most organs in a species of fish, studies of seabirds indicate that the size of organs can vary dramatically among populations of the same species, some of which may be a result of adaptation to local conditions (Hilton et al. 2000). For instance, metabolic supply and processing organs, such as liver and pyloric caeca, may be relatively large under circumstances where individuals can allocate a greater proportion of their acquired energy intake to somatic growth instead of activity (Bergot et al. 1981; Magnan and Stevens 1992). Similarly, a larger heart muscle is expected in populations that have relatively high activity levels (Farrell et al. 1990). In our study, we predicted stream populations of rainbow trout that must actively swim against a current to have relatively large heart sizes for a given body size. In contrast with processing and circulatory organs, the size of digestive organs has been examined extensively in fishes. Herbivorous and omnivorous fish species, which exploit a food source with a relatively low energy density, tend to have a larger gut size than piscivorous species that feed on prey with a high energy density (Fryer and Iles 1972; Kramer and Bryant 1995). Hence, piscivorous rainbow trout populations were predicted to have relatively small intestines compared with omnivorous populations.

To test our predictions, we devised a sampling program to compare replicate rainbow trout populations from eight putative ecotypic categories that were selected based on habitat characteristics or the composition of fish species present. We used populations from British Columbia, Canada, because this area represents a core of the natural distribution for this species that also has numerous populations that are unaffected by artificial stocking. We established three of these ecotypes based on observations of past researchers, which include large-lake "piscivores" (Irvine 1978), "headwater" (stream) populations (Northcote and Hartman 1988), and "anadromous" populations, commonly referred to as steelhead trout (Withler 1966; Smith 1969). In addition to the first two stream-dwelling ecotypes (headwater and anadro-

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mous populations), we also included a "large river" ecotype representing populations that achieve a relatively large body size at maturity but do not have access to the ocean (Northcote 1997). Because competition is thought to be an important force in driving differentiation (Magnan 1988; Schluter and McPhail 1993; Robinson and Wilson 1994), we also compared rainbow trout populations from lakes with different combinations of competitors. As a basis of comparison, we sampled lakes where rainbow trout were the only fish species present (solitary populations) as well as populations with different combinations of competitors. Hence, three types of mixed species lakes were included in our ecotypic comparisons. We sampled rainbow trout populations that only co-occur with either a sucker species (Catostomidae) as a benthos competitor (mixed 1) or a minnow species (Cyprinidae) as a plankton and benthos competitor (mixed 2) as well as populations with both types of competitors (mixed 3).

Finally, we also examined rainbow trout populations over a smaller scale by sampling interconnected streams and lakes within replicate watersheds. We compared the results from the large and small spatial scales to determine whether differences across large spatial scales can be used to predict differences at local scales where population and habitat characteristics are less well known. Given the growing and widespread threats of extinction in many ecosystems, our study provides a method of mapping biodiversity at the intraspecific level using ecologically based hypotheses and the knowledge of the aquatic landscape that each population inhabits.

Methods and materials

We attempted to sample at least three replicate populations of each of the eight putative ecotypes across a wide geographic area (Fig. 1*a*). The ecotypes sampled were solitary, piscivorous, mixed 1, mixed 2, and mixed 3 lake populations as well as headwater, large river, and anadromous stream populations (Table 1). We sampled over two different geographic scales. Our initial sample of 34 populations spanned 600 000 km^2 of British Columbia, while our second level of sampling involved 27 populations within the Nechako River watershed covering about 2000 km^2 (Fig. 1*b*). We initiated our search for populations that had a specific composition of fish species by using a database that provides a list of species present in water bodies across British Columbia (http://www.bcfisheries.gov.bc.ca/fishinv). Because we were only interested in examining natural populations, we also used the database to eliminate rainbow trout populations that had been established by artificial stocking or had been repeatedly stocked with rainbow trout from nonnative populations. We used this initial list to identify potential sample sites and we then queried regional government biologists to determine whether our species list was correct and whether populations had been artificially established or supplemented but were unreported in the database.

To collect the full range of age-classes present in each population, we used a variety of techniques to capture rainbow trout. In streams that had a maximum depth of less than 1 m, we used a backpack electroshocker to sample fish up to 30 cm. In larger streams or rivers that had age-classes of fish that occupied habitats too deep to be reached by someone wading with an electroshocker, we collected individuals by angling. In lake populations, we collected individuals by using a monofilament gill net or by angling. Each of 135-m gill nets consisted of 15-m panels of netting that varied in mesh size from 1.3 to 9 cm. By using a multipanel net, we were able to collect fish down to 5 cm in length as well as the largest individuals in the population. In addition, we used a 2 m by 25 m beach seine, with 5-mm mesh, to encircle and capture smaller individuals found in the littoral region of a lake. In most lake populations, we captured 50 individual rainbow trout distributed across as many age-classes as we could capture. In populations with a narrow range of age- and size-classes, we limited our sample to 35 individuals.

We held all captured individuals in a holding container with fresh water until we measured each fish for fork length (±1 mm) and mass (±0.01 g), collected a scale sample for aging and a tissue sample stored in 95% ethanol for archiving and DNA analysis (P. Tamkee and E.B. Taylor, Department of Zoology, The University of British Columbia, Vancouver, British Columbia, unpublished data), and then attached a unique identification tag to each fish. We euthanized fish before collecting size measurements and then finally placed individuals in preservative (10% formalin) for later morphometric analyses. In the laboratory, we measured external morphological characteristics using a digital caliper (±0.01 mm) connected to a microcomputer that compiled all measurements electronically. We selected a suite of external morphological features that reflected characteristics of the fish that we hypothesized would be selected for under different ecotypic conditions (Fig. 2). For comparing differences in feeding morphology, we used measurements of mouth, eye, and head dimensions, whereas swimming morphology was assessed by comparing differences in paired fin length, caudal peduncle depth, and body depth (Boily and Magnan 2002). We calculated average gill raker spacing and length for each individual by removing the left-most gill arch and measuring the length and distance between all rakers on the arch with a dissecting microscope. To assess ecotypic differences in internal organ investment, we measured the mass of heart, liver, pyloric caeca, stomach, and intestine. We measured the mass of internal organs of the preserved fish by clipping off the esophagus and circulatory system at the level of the esophageal sphincter and removing the viscera from the body cavity. We separated individual organs and any fatty tissue from each other and then weighed each organ on an electronic balance (±0.0001 g). The heart was separated from the circulatory system by clipping off the organ at the narrowing of the bulbous arteriosus or the origin of the ventral aorta and removing it from the pericardial sac. The intestine was clipped off from the lower region of the stomach at the pyloric sphincter and any contents were removed before being weighed. The liver and pyloric caeca were cut from the point of attachment to the viscera, whereas the gonads were separated at the point of attachment to the mesonephric duct. All measurements were made on moist specimens that had excess water removed by momentarily blotting organs with a paper towel.

Statistical analyses

To correct for size-related differences across individuals and populations, we regressed each morphological character-

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Fig. 1. (*a*) Geographic locations of 34 rainbow trout (*Oncorhynchus mykiss*) populations included in the large-scale comparison of trout morphology. Numbers 1–34 identify the populations and correspond to those listed in Appendix A. The hatched box depicts the area represented in Fig. 1*b*. The inset map identifies the location of British Columbia within the native distribution (shaded area) of rainbow trout in North America. (*b*) Geographic locations of 27 rainbow trout populations from interconnected lakes and streams used in the small-scale comparisons examining trout morphology. Numbers 35–61 identify the populations and correspond to those listed in Appendix A.

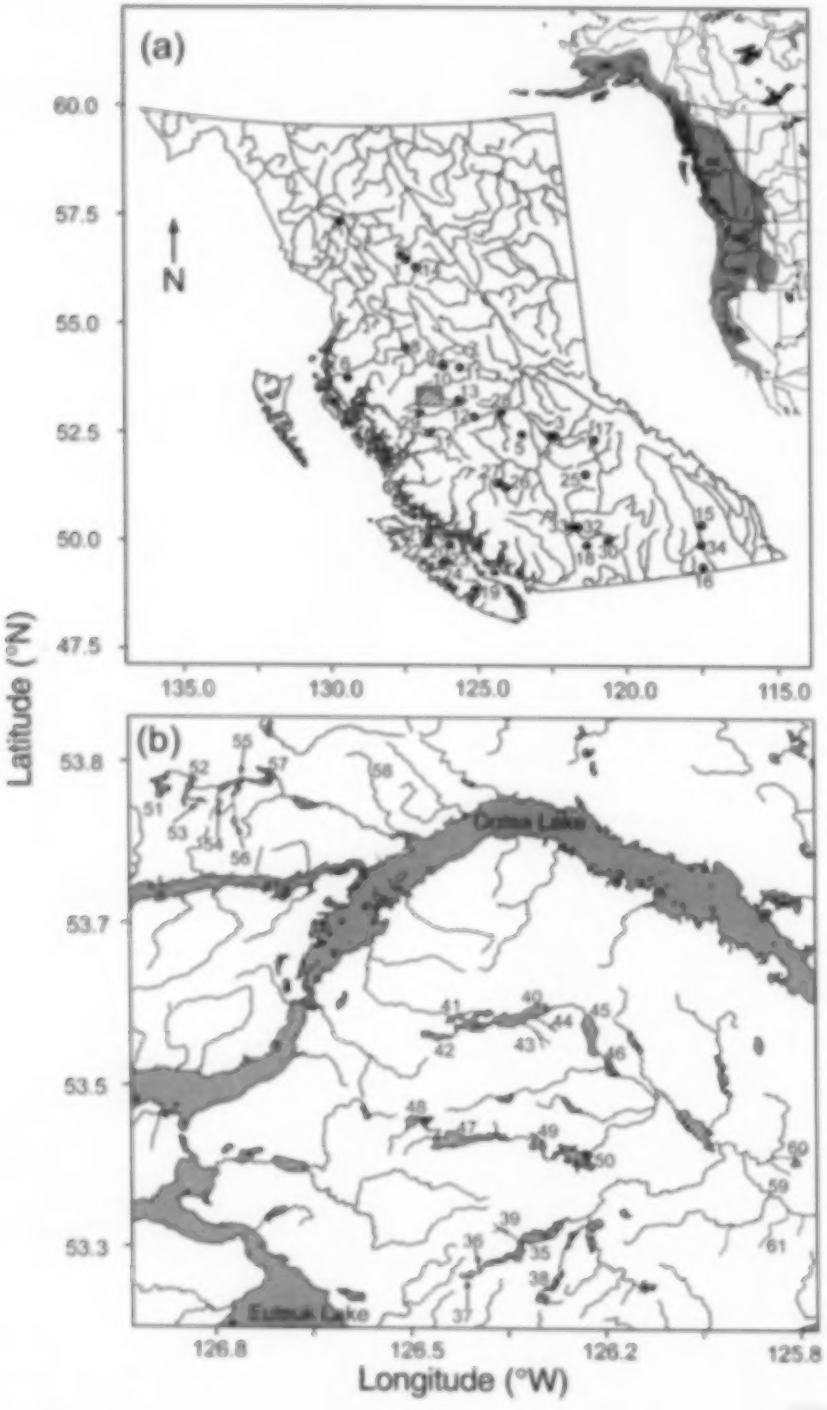

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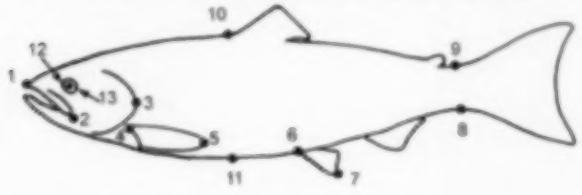
Table 1. Ecotypic categories and defining criteria used in comparing rainbow trout (*Oncorhynchus mykiss*) morphology from British Columbia lakes and streams.

Ecotype	Habitat type	Ecological criteria	Reference(s)[a]
Solitary	Lake	Rainbow trout only fish species present	Bourke et al. 1999
Mixed 1	Lake	Rainbow trout with benthivorous fish species present (Catostomidae)	Magnan 1988
Mixed 2	Lake	Rainbow trout with planktivorous fish species present (Cyprinidae)	Johannes and Larkin 1961
Mixed 3	Lake	Rainbow trout with planktivorous and benthivorous fish species present	Magnan 1988; Johannes and Larkin 1961
Piscivore	Lake	Piscivorous rainbow trout	Irvine 1978
Headwater	Stream	First-order stream located above a movement barrier	Northcote and Hartman 1988
Large river	Stream	Fifth-order stream or larger located above a fish movement barrier	Northcote 1997
Anadromous	Stream	Population that migrates between a freshwater and marine habitat	Withler 1966; Smith 1969

[a]Past studies that have noted putative ecotypes for rainbow trout or morphological or ecological differentiation for a similar species of salmonid fish.

Fig. 2. Position of the landmarks used to measure the size of rainbow trout (*Oncorhynchus mykiss*) morphological features. Features are defined as follows: 1–2, premaxilla length; 1–3, head length; 4–5, pectoral fin length; 6–7, pelvic fin length; 8–9, caudal peduncle depth; 10–11, body depth; 12–13, eye diameter. Other morphological measures not shown include head width (the distance between the left and right side of the head measured at the center of the opercula), mouth width (the internal breadth of the mouth measured proximate to point 2 on either side of the buccal cavity), and gill raker length and spacing.



istic against fork length. All measurements were $\log_{10}$ transformed to ensure that we met the assumption of homogeneity of variance, and we visually examined the residuals from all analyses by plotting them against body size to ensure that we met this assumption. Because of the large number of pairwise comparisons of slopes, we could not assume that the slope describing the relationship between morphological traits and body size was equal across all populations. We used the population or separate within-group slope to adjust each trait to a common body size based on the method of Thorpe (1976). We calculated size-adjusted measurements for internal organs in the same manner except that we used the mass of organs regressed against fish body mass to calculate the slope used to estimate the size-adjusted trait.

Based on our preliminary survey of government databases, we identified and sampled a target of three populations from each of the eight ecotypes. We discovered, however, that in some cases, the species composition was slightly different from that recorded in the databases. Some lake populations had more species present than anticipated, resulting in more than three populations in some mixed species lake ecotypes. We were also able to identify and sample only two populations of two categories that contained rainbow trout with one other fish species: rainbow trout with a sucker species or rainbow trout with a minnow species. In all other categories, we obtained at least three populations of each ecotype (Fig. 1*a*; Appendix A).

To assess overall morphological differences between ecotypes, we used a multivariate analysis of variance (MANOVA) for size-adjusted external features (including gill raker length and spacing) and a separate MANOVA for internal organs that were also size adjusted. In our MANOVA models, we used ecotype as one independent variable and population nested within ecotype as a second variable to determine whether our approach of using a population as a unit of observation provided meaningful comparisons even after controlling for variability among individuals within populations. To provide an objective summary of correlated differences across rainbow trout populations, we performed a principal component analysis (PCA) of correlation matrices on the size-adjusted data to determine whether morphological variation in swimming, feeding, and organ size was related to ecotypic variation (Fleming et al. 1994). We only considered PCs with eigenvalues greater than 1 (Quinn and Keough 2002). When rotation of principal axes improved their interpretation, we used a promax rotation method (SAS Institute Inc. 1999). We compared variation in PC scores with a nested analysis of variance (ANOVA) to determine whether a significant proportion was accounted for by ecotypic differences or by populations nested within ecotypes. For nested ANOVA computations, we used the mixed-model procedure (proc mixed) with ecotype as a fixed effect and population as a random effect in SAS version 8.02, which employs a restricted maximum likelihood estimation (SAS Institute Inc. 1999) to evaluate the effect of population nested within ecotype. Tests of significance for random effects in nested ANOVA models were based on the likelihood ratio (LR) statistic (Littell et al. 1996). To calculate the variance components in nested models, we used the general linear model procedure (proc glm) for fixed effects and the variance component procedure (proc varcomp) for random effects (SAS Institute Inc. 1999). All ecotypic comparisons (fixed effects) were based on the variation remaining after statistically controlling for the effect of population

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Table 2. Results from univariate nested ANOVA for 11 morphological characteristics of rainbow trout (*Oncorhynchus mykiss*), comparing the variation accounted for among populations nested within ecotypes or among ecotypes.

		Large-scale variation		Small-scale variation	
Morphological trait	Variance component	% of total variation	*P*	% of total variation	*P*
Caudal peduncle depth	Among populations within ecotypes	19.7	0.0005	40.9	0.0001
	Among ecotypes	28.8	0.0001	6.92	0.42
Body depth	Among populations within ecotypes	33.7	0.0003	30.8	0.0001
	Among ecotypes	26.6	0.0011	7.95	0.22
Pectoral fin length	Among populations within ecotypes	21.8	0.0004	44.9	0.0001
	Among ecotypes	37.8	0.0001	27.1	0.0098
Pelvic fin length	Among populations within ecotypes	25.8	0.0004	26.8	0.0001
	Among ecotypes	35.0	0.0001	28.1	0.0004
Head length	Among populations within ecotypes	31.1	0.0003	35.1	0.0001
	Among ecotypes	20.5	0.011	28.9	0.0001
Head width	Among populations within ecotypes	23.2	0.0004	26.5	0.0001
	Among ecotypes	19.2	0.0016	42.4	0.0001
Mouth width	Among populations within ecotypes	24.5	0.0004	25.8	0.0001
	Among ecotypes	30.3	0.0001	24.3	0.0009
Premaxilla length	Among populations within ecotypes	24.8	0.0004	44.5	0.0001
	Among ecotypes	32.1	0.0001	24.7	0.016
Eye diameter	Among populations within ecotypes	36.6	0.0003	61.7	0.0001
	Among ecotypes	52.9	0.0001	22.2	0.074
Gill raker length	Among populations within ecotypes	18.2	0.0006	40.6	0.0001
	Among ecotypes	17.8	0.0007	0.6	0.98
Gill raker spacing	Among populations within ecotypes	80.0	0.0002	33.3	0.0001
	Among ecotypes	11.5	0.68	9.2	0.15

Note: Large-scale variation refers to 34 populations sampled across British Columbia, and small-scale variation refers to 27 populations sampled within a single watershed. All traits were adjusted to a common body size of 179 mm (fork length) for the large-scale data set and 208 mm (fork length) for the small-scale data set.

nested within ecotype. If we made inferences about all possible pairwise comparisons simultaneously, we employed a false discovery rate method to avoid the problem of type I errors in our analyses (Benjamini and Hochberg 1995; García 2003).

Finally, as a measure of the predictive power of our morphological measurements in distinguishing our hypothesized ecotypes, we used a linear combination of external features or internal organ sizes in discriminant function analyses to determine if we could reliably predict ecotype membership of a population based on average population scores.

Results

Swimming and feeding morphology

Our analysis of size-adjusted morphology indicated that there were significant differences in rainbow trout morphology both among populations within ecotypes and among ecotypes. When all size-adjusted external measurements were combined in a nested MANOVA, significant differences in morphology were found among rainbow trout ecotypes (Wilks' $\lambda = 0.00075$, $F_{[77,103]} = 3.12$, $P < 0.0001$) and among populations nested within ecotypes (Wilks' $\lambda = 0.022$, $F_{[286,15579]} = 24.99$, $P < 0.0001$). In addition to the overall measure of morphological differentiation, 10 of 11 morphological features showed significant levels of differentiation among ecotypes based on univariate nested ANOVA, and all 11 characteristics had a significant, additional component of variation accounted for by the effect of population nested within ecotype (Table 2). On average, among-ecotype effects accounted for 28.4% of the variation in morphological traits (range = 11.6%–52.9%), whereas among-population within-ecotype effects accounted for 25.6% (range = 18.2%–80.0%) (Table 2).

When we summarized morphological differences by PCA, some but not all ecotypic categories were separated from each other based on PC scores. Four principal axes with eigenvalues greater than 1 were extracted from the PCA summarizing relative differences in morphological features (Table 3*a*). Across ecotypes, the most distinct separation occurred along the first axis between the three stream and five lakes ecotypes (Fig. 3*a*). A nested ANOVA of PC scores from the first axis revealed that 34.9% of the variation was accounted for by among-ecotype differences ($F_{[7,26]} = 8.07$, $P < 0.0001$) and 31.3% of the variation was accounted for by among-population within-ecotype differences (LR = 379.8, $P < 0.0001$). The suite of morphological features that loaded most strongly along the first axis indicated that stream and piscivorous populations had relatively large head and eye dimensions (Table 3*a*). Based on PC scores from the second axis, 40.9% of the variation was accounted for by among-ecotype differences ($F_{[7,26]} = 15.94$, $P < 0.0001$) and 20.6% of the variation was accounted for by among-population within-ecotype differences (LR = 222.3, $P < 0.0001$). The second principal axis separated groups primarily based on fin length and gill raker length (Table 3*a*). The

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Table 3. Loading coefficients from a principal component analysis (PCA) for (*a*) 11 external characteristics (including gill raking length and spacing) and (*b*) from a second PCA for five internal organ characteristics of 34 rainbow trout (*Oncorhynchus mykiss*) populations.

Morphological variable	PC 1	PC 2	PC 3	PC 4
(*a*) External characteristics				
Caudal peduncle depth	0.28	0.17	0.73	–0.14
Body depth	–0.058	–0.045	0.92	0.10
Pectoral fin length	0.36	0.57	0.24	–0.14
Pelvic fin length	0.28	0.52	0.37	0.023
Head length	0.87	–0.0043	0.046	0.101
Premaxilla length	0.88	0.038	–0.071	0.09
Mouth width	0.81	0.046	0.066	0.081
Head width	0.74	–0.089	0.19	–0.097
Eye diameter	0.49	0.51	–0.31	–0.19
Gill raker length	–0.16	0.86	0.0036	0.20
Gill raker spacing	0.09	0.058	–0.011	0.97
Eigenvalue	4.67	1.49	1.12	1.025
Proportion of total	0.42	0.14	0.102	0.093
(*b*) Internal organs				
Stomach mass	0.57	0.56	–0.46	–0.38
Pyloric caeca mass	0.83	–0.27	0.12	0.17
Intestine mass	0.79	–0.16	–0.36	0.35
Liver mass	0.73	–0.15	0.52	–0.35
Heart mass	0.16	0.87	0.36	–0.3
Eigenvalue	2.21	1.18	0.76	0.51
Proportion of total	0.44	0.24	0.15	0.10

Note: Eigenvalues from each PC are listed below the column of coefficients.

third axis loaded most strongly on caudal peduncle and body depth (Table 3*a*). Based on PC scores from the third axis, 34.1% of the variation was accounted for by among-ecotype differences ($F_{[7,26]} = 6.59$, $P = 0.0002$) and 33.8% of the variation was accounted for by among-population within-ecotype differences (LR = 379.0, $P < 0.0001$). The fourth axis loaded most strongly on gill raker spacing (Table 3*a*); 18.6% of the variation was accounted for by ecotypic differences ($F_{[7,26]} = 1.34$, $P = 0.27$), whereas 75.3% of the variation was accounted for by among-population within-ecotype differences (LR = 1766.3, $P < 0.0001$)

When all eight ecotypes were compared against each other along the first principal axis, two separate groups comprising all stream ecotypes as well as piscivorous and mixed 1 ecotypes were distinguished from all remaining lake ecotypes (Fig. 3*a*). Based on scores from the second axis, anadromous and headwater ecotypes were distinguished from all other ecotypes (Fig. 3*a*). Although stream ecotypes were not significantly separated from each other based on scores from the first principal axis ($F_{[2,12]} = 0.27$, $P = 0.77$), when all stream ecotypes were compared against all lake ecotypes, stream ecotypes had higher scores than lake ecotypes ($F_{[1,32]} = 46.99$, $P < 0.0001$) (Fig. 3*a*). In contrast, piscivorous lake ecotypes could not be distinguished from stream populations ($F_{[1,26]} = 1.32$, $P = 0.26$) but did have higher scores than other lake ecotypes ($F_{[1,26]} = 6.89$, $P = 0.014$) (Fig. 3*a*). Along the second principal axis, stream ecotypes had significantly higher scores than lake ecotypes ($F_{[1,32]} = 61.80$, $P < 0.0001$) and were highest for anadromous and headwater populations in comparison with all other ecotypes (Fig. 3*a*). The third axis, primarily distinguishing caudal peduncle and body depth, could not differentiate stream and lake ecotypes ($F_{[1,32]} = 0.35$, $P = 0.56$); however, headwater populations had higher scores than all other ecotypes except large river populations (Fig. 3*b*). Given that there was no additional component of variation accounted for by ecotypic differences along the fourth axis, we did not consider it further.

Internal organ size

Our analysis of internal organs indicated that there were significant differences in rainbow trout organ size both among populations within ecotypes and among ecotypes. When the mass of all size-adjusted organs were combined in a nested MANOVA, significant differences in organ size were found among rainbow trout ecotypes (Wilks' $\lambda = 0.081$, $F_{[35,95]} = 2.22$, $P = 0.0012$) and among populations nested within ecotypes (Wilks' $\lambda = 0.16$, $F_{[130,7474]} = 26.42$, $P < 0.0001$). Three of five features showed significant levels of differentiation among ecotypes based on univariate nested ANOVA (Table 4). All five characteristics had a significant additional component of variation accounted for by the effect of population nested within ecotype (Table 4). On average, among-ecotype effects accounted for 22.8% of the variation in organ sizes (range = 9.1%–42.6%), whereas among-population within-ecotype effects accounted for 40.0% of the variation (range = 17.7%–57.8%) (Table 4).

Two principal axes with eigenvalues greater than 1 were extracted from the PCA summarizing relative differences in organ size (Table 3*b*). All internal organs except heart mass

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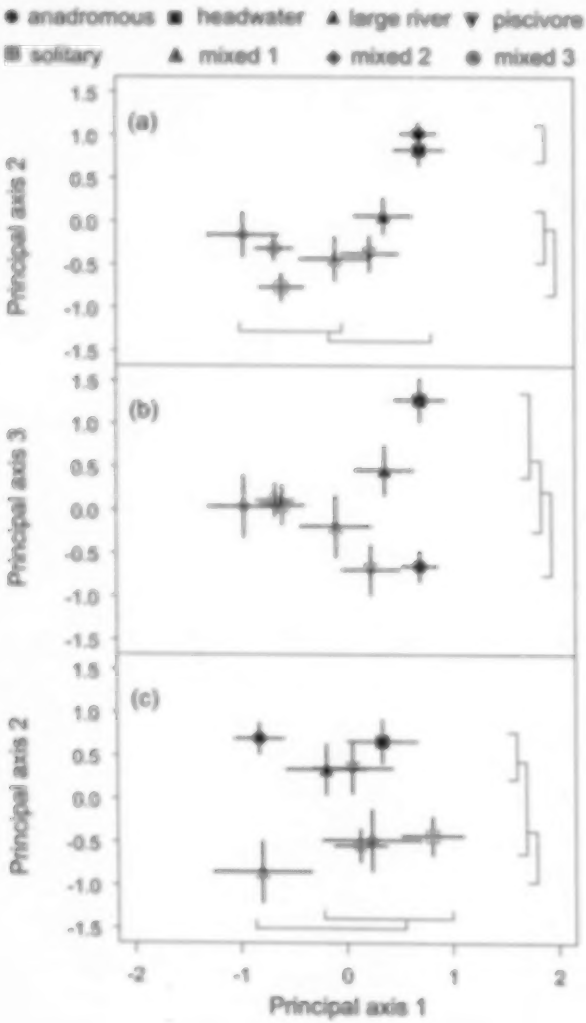
Fig. 3. Mean principal component scores (±1 SE) based on 11 morphological characteristics for eight ecotypic categories of 34 rainbow trout (*Oncorhynchus mykiss*) populations comparing (*a*) axis 1 versus axis 2 and (*b*) axis 1 versus axis 3. (*c*) Mean principal component scores (±1 SE) based on five internal organ sizes for eight ecotypic categories of 34 rainbow trout populations comparing axis 1 versus axis 2. Note that Fig. 3*c* represents scores from a completely separate principal component analysis than in Fig. 3*a* or Fig. 3*b*. Means that are not significantly different from each other on either axis (pairwise adjusted $P > 0.05$) share both a common vertical and a common horizontal line within the plot area.



loaded strongly along the first axis, whereas heart mass and stomach mass loaded strongly along the second axis (Table 3*b*). A nested ANOVA of PC scores along the first axis found that 29.7% of the variation was accounted for by among-ecotype differences ($F_{[7,26]} = 3.42$, $P = 0.010$) and 54.9% of the variation was accounted for by among-population within-ecotype differences (LR = 932.0, $P < 0.0001$). When all eight ecotypes were compared along the first axis, only solitary populations could be distinguished from anadromous, large river, and mixed 1 ecotypes (Fig. 3*c*). Despite the overlap in scores across the first axis, when all lake ecotypes were compared against all stream ecotypes, lake ecotypes (mean PC score = 0.21) had higher scores than stream ecotypes (mean PC score = –0.39; $F_{[1,26]} = 4.96$, $P = 0.033$). Based on PC scores from the second axis, 23.1% of the variation was accounted for by among-ecotype differences ($F_{[7,26]} = 5.96$, $P = 0.0003$) and 33.8% of the variation was accounted for by among-population within-ecotype differences (LR = 374.8, $P < 0.0001$). When compared along the second principal axis, stream and piscivorous ecotypes were most similar but were only significantly different from mixed 1 ecotypes.

Discriminant analyses

Using the 11 size-adjusted external features, three significant canonical axes were extracted from our discriminant analysis, resulting in correct classification of the putative ecotypes in 32 of 34 populations (94%) and accounting for 91.1% of the morphological variation between ecotypes (Table 5*a*). The only misclassifications occurred between two lake populations, when one mixed 3 population was misclassified as a piscivorous population and one solitary population was misclassified as a mixed 2 population. Stream-dwelling populations were most strongly differentiated from other ecotypes by the first canonical axis, which loaded positively on nine of 11 characteristics (Table 5*a*; Fig. 4*a*). Piscivorous populations were primarily differentiated along the third canonical axis based on relatively large head features such as premaxilla length, head length, and mouth width (Table 5*a*; Fig. 4*b*).

When we performed a discriminant analysis using internal organ sizes to differentiate rainbow trout ecotypes, we were less successful at predicting group membership. Only the first axis accounted for a significant proportion of the variation in morphology, successfully classifying ecotype membership in 27 of 34 cases or a 79.4% success rate (Table 5*b*). Discriminant analyses of internal organ features were best at separating stream versus lake ecotypes, but within each of these two general categories, the groups were often intermixed (Fig. 4*c*).

Small-scale variation in morphology

On a smaller spatial scale, we found that most lakes or streams sampled within a watershed tended to have a similar species composition. Of the 27 interconnected lakes or streams sampled, 21 lakes had a rainbow trout population sympatric with at least one species of benthivorous and planktivorous fish (a mixed 3 ecotype) and were usually composed of the same species (Fig. 1*b*; Appendix A). Two lakes had solitary populations of rainbow trout and two streams had headwater populations isolated above an upstream migration barrier. Only the largest river in one subwatershed supported a large river population of rainbow trout. As with the large-scale data set, a significant component of variation in morphological traits was accounted for by populations nested within ecotypes (MANOVA, Wilks' $\lambda = 0.021$, $F_{[231,10999]} = 21.01$, $P < 0.0001$) and a marginal amount among ecotypes (MANOVA, Wilks' $\lambda = 0.027$, $F_{[44,44.04]} = 1.57$, $P = 0.070$). In addition to the overall mea-

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Table 4. Results from univariate nested ANOVA for five internal organ characteristics of rainbow trout (*Oncorhynchus mykiss*) comparing the variation accounted for among populations nested within ecotypes or among ecotypes.

		Large-scale variation		Small-scale variation	
Morphological trait	Variance component	% of total variation	*P*	% of total variation	*P*
Stomach mass	Among populations within ecotypes	57.8	0.0002	51.4	0.0007
	Among ecotypes	27.9	0.034	23.5	0.030
Pyloric caeca mass	Among populations within ecotypes	49.9	0.0002	31.6	0.0010
	Among ecotypes	42.6	0.0001	9.4	0.14
Intestine mass	Among populations within ecotypes	41.2	0.0003	50.5	0.0007
	Among ecotypes	22.5	0.018	4.3	0.74
Liver mass	Among populations within ecotypes	33.5	0.0003	25.2	0.0013
	Among ecotypes	12.1	0.11	8.2	0.13
Heart mass	Among populations within ecotypes	17.7	0.0011	29.9	0.0010
	Among ecotypes	9.1	0.097	8.8	0.16

Note: Large-scale variation refers to 34 populations sampled across British Columbia, and small-scale variation refers to 27 populations sampled within a single watershed. All traits were adjusted to a common body mass of 143 g for the large-scale data set and 134 g for the small-scale data set.

Table 5. Loading coefficients from a discriminant analysis for (*a*) 11 external characteristics (including gill raking length and spacing) and (*b*) from a second discriminant analysis for five internal organ characteristics of 34 rainbow trout (*Oncorhynchus mykiss*) populations from across British Columbia.

Morphological variable	Canonical axis 1	Canonical axis 2	Canonical axis 3
(*a*) External characteristics			
Caudal peduncle depth	0.53	0.64	0.11
Body depth	–0.17	0.54	0.14
Pectoral fin length	0.81	0.20	0.31
Pelvic fin length	0.61	0.43	0.45
Head length	0.51	–0.04	0.55
Premaxilla length	0.69	–0.103	0.58
Mouth width	0.78	0.093	0.36
Head width	0.66	0.14	–0.15
Eye diameter	0.90	–0.201	0.0019
Gill raker length	0.69	–0.23	–0.26
Gill raker spacing	–0.33	0.042	0.202
Eigenvalue	14.71	3.66	2.62
Proportion of total	0.64	0.16	0.11
(*b*) Internal organs			
Stomach mass	–0.34	0.74	0.51
Pyloric caeca mass	0.82	0.48	0.26
Intestine mass	0.64	0.34	0.58
Liver mass	0.54	0.304	0.54
Heart mass	–0.56	0.302	0.37
Eigenvalue	3.78	0.92	0.27
Proportion of total	0.75	0.18	0.054

sure of morphological differentiation, six of 11 morphological features showed significant levels of differentiation among ecotypes based on univariate nested ANOVA, and all 11 characteristics had a significant, additional component of variation accounted for by the effect of population nested within ecotype. On average, among-ecotype effects accounted for 20.2% of the variation in morphological traits (range = 0.6%–42.4%), whereas among-population within-ecotype effects accounted for 37.4% (range = 24.3%–61.7%) (Table 2).

In comparison with the large-scale data set, we again found similar morphological differences by ecotypic category when the traits were summarized by PCA groupings. Stream populations had significantly larger PC scores based on the first PC axis ($F_{[1,24]} = 30.00$, $P < 0.0001$) (Fig. 5*a*), which loaded most strongly on fin length and head dimensions (Table 6). A nested ANOVA of PC scores from the first axis revealed that 46.3% of the variation was accounted for by among-ecotype differences ($F_{[4,21]} = 8.54$, $P = 0.0003$) and 48.7% of the variation was accounted for by differences

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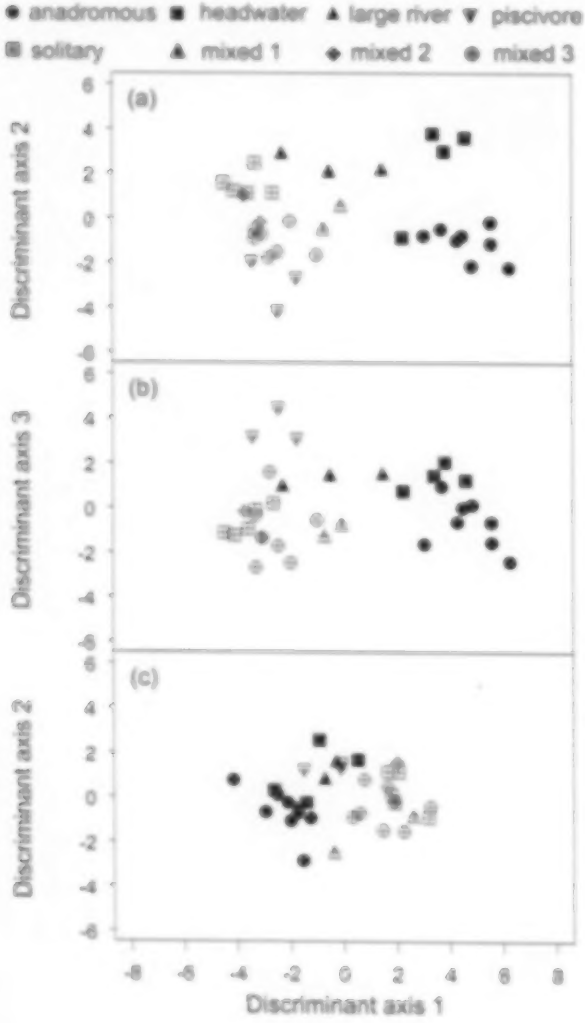
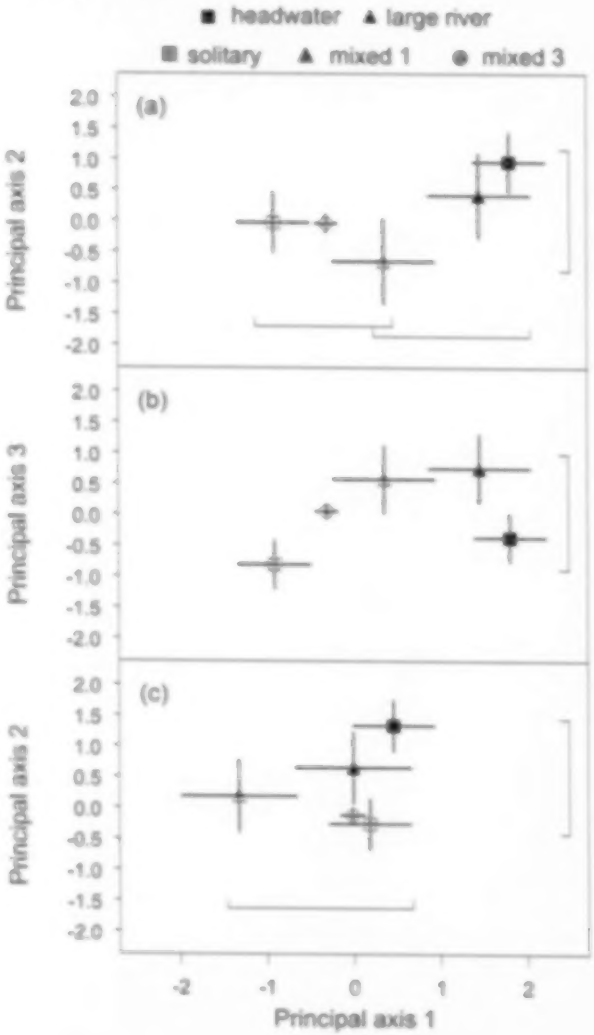
Fig. 4. Canonical scores based on 11 morphological features from a discriminant analysis of 34 rainbow trout (*Oncorhynchus mykiss*) populations for (*a*) axis 1 versus axis 2 and (*b*) axis 1 versus axis 3 across eight ecotypic categories. (*c*) Canonical scores based on five internal organ size characteristics from a discriminant analysis of 34 rainbow trout populations for axis 1 versus axis 2 across eight ecotypic categories. Note that Fig. 4*c* represents scores from a completely separate discriminant analysis than in Fig. 4*a* or Fig. 4*b*.



among populations nested within ecotypes (LR = 449.6, $P < 0.0001$). Based on PC scores from the second axis, 9.9% of the variation was accounted for by among-ecotype differences ($F_{[4,21]} = 1.81$, $P = 0.16$) and 47.8% of the variation was accounted for by differences among populations nested within ecotypes (LR = 565.4, $P < 0.0001$). The second principal axis provided weak separation of groups primarily based on caudal peduncle and body depth (Table 6*a*). The third axis loaded most strongly on gill raker spacing. Based on PC scores from the third axis, 9.1% of the variation was accounted for by among-ecotype differences ($F_{[4,21]} = 1.72$, $P = 0.18$), whereas 31.2% of the variation was accounted for by among-population within-ecotype differences (LR = 315.1, $P < 0.0001$).

Fig. 5. Mean principal component scores (±1 SE) based on 11 morphological characteristics for eight ecotypic categories of 27 rainbow trout (*Oncorhynchus mykiss*) populations comparing (*a*) axis 1 versus axis 2 and (*b*) axis 1 versus axis 3. (*c*) Mean principal component scores (±1 SE) based on five internal organ sizes for eight ecotypic categories of 27 rainbow trout populations comparing axis 1 versus axis 2. Note that Fig. 5*c* represents scores from a completely separate principal component analysis than in Fig. 5*a* or Fig. 5*b*. Means that are not significantly different from each other on either axis (pairwise adjusted $P > 0.05$) share both a common vertical and a common horizontal line within the plot area except in Fig. 5*c* for headwater versus mixed 3 populations, which were different based on the second principal axis.



Our analysis of internal organs on the small-scale data set indicated that there were significant differences in rainbow

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Table 6. Loading coefficients from a principal component analysis (PCA) for (*a*) 11 external characteristics and (*b*) from a second PCA for five internal organ characteristics of 27 rainbow trout (*Oncorhynchus mykiss*) populations from within a single watershed.

Morphological variable	PC 1	PC 2	PC 3
(*a*) External characteristics			
Caudal peduncle depth	0.1006	0.83	–0.0059
Body depth	–0.053	0.85	–0.086
Pectoral fin length	0.80	–0.073	–0.23
Pelvic fin length	0.80	–0.03	–0.23
Head length	0.85	0.12	0.081
Premaxilla length	0.80	0.088	0.074
Mouth width	0.71	0.05	0.12
Head width	0.63	0.38	0.11
Eye diameter	0.68	–0.13	0.16
Gill raker length	–0.014	0.076	0.25
Gill raker spacing	0.028	–0.049	0.93
Eigenvalue	4.45	1.57	1.12
Proportion of total	0.41	0.14	0.10
(*b*) Internal organs			
Stomach mass	0.7	–0.047	–0.61
Pyloric caeca mass	0.53	–0.39	0.67
Intestine mass	0.83	–0.28	0.082
Liver mass	0.42	0.62	0.34
Heart mass	0.28	0.77	–0.00068
Eigenvalue	1.7	1.21	0.94
Proportion of total	0.34	0.24	0.19

trout organ size among populations nested within ecotypes but not among ecotypes. When all size-adjusted organs were combined in a nested MANOVA, there were no significant differences in organ size among the five rainbow trout ecotypes (Wilks' $\lambda = 0.22$, $F_{[20,57.3]} = 1.64$, $P = 0.075$). One of the five features exhibited significant levels of differentiation among ecotypes based on univariate nested ANOVAs (Table 4). A significant proportion of morphological variation was, however, accounted for by differences among populations nested within ecotypes (Wilks' $\lambda = 0.13$, $F_{[105,572.5]} = 28.31$, $P < 0.0001$, and all five characteristics had a significant additional component of variation accounted for by the effect of population nested within ecotype (Table 4). On average, among-ecotype effects accounted for 10.8% of the variation in morphological traits (range = 4.3%–51.4%), whereas among-population within-ecotype effects accounted for 31.3% of the variation (range = 25.2%–50.4%) (Table 4).

Two principal axes with eigenvalues greater than 1 were extracted from the PCA summarizing relative differences in organ size (Table 6*b*). All internal organs loaded strongly along the first axis, and heart and liver size loaded strongly along the second axis (Table 6*b*). Based on a nested ANOVA of PC scores from the first axis, 9.2% of the variation was accounted for by among-ecotype effects ($F_{[4,21]} = 1.24$, $P = 0.33$) and 45.5% of the variation was accounted for by among-population within-ecotype effects (LR = 575.0, $P < 0.0001$). When compared along the second PC axis, 17.3% of the variation was accounted for by among-ecotype effects ($F_{[4,21]} = 3.18$, $P = 0.035$) and 38.5% of the variation by among-population within-ecotype effects (LR = 442.9, $P < 0.0001$). The relatively low proportion of variation accounted for by ecotypic differences in organ size was reflected in the overlap of PC scores when compared by ecotype (Fig. 5*c*). We could not detect any significant difference among ecotypes along the first axis ($F_{[4,22]} = 1.24$, $P = 0.33$). There were, however, differences across the second axis ($F_{[4,22]} = 3.18$, $P = 0.035$): stream ecotypes had higher scores than lake ecotypes ($F_{[1,24]} = 12.32$, $P = 0.0018$) (Fig. 5*c*). Based on pairwise comparisons, only headwater ecotypes could be distinguished from mixed 3 ecotypes along the second principal axis (Fig. 5*c*).

We also applied the discriminant function from the large-scale data set to classify the small-scale data set and to test its applicability to an unrelated sample based on external characteristics. Despite similar patterns in morphology-based PC scores and the high predictive ability of the large-scale data set in correctly classifying ecotypic category, the success was not as high when the large-scale discriminant function was applied to the interconnected system of streams and lakes. Although all stream populations were correctly classified as stream ecotypes and 22 of 24 lake populations were correctly classified as lake ecotypes, only 19 of 27 populations in the small-scale data set were correctly classified by the large-scale discriminant function. Four lake populations were assigned to an incorrect lake category and two were assigned as stream ecotypes. In addition, one headwater stream population was assigned as an anadromous ecotype and the large river population was assigned as a headwater ecotype.

Discussion

Our data indicate that a significant proportion of morphological variation among rainbow trout populations is associated with our hypothesized ecotypic categories, with the largest differences occurring between stream- and lake-dwelling populations. Several observations suggest that the differences in body and fin morphology between stream and lake populations are adaptive responses to differences in water velocity. Salmonids often use their pectoral fins as hydrofoils to minimize energy expenditure in streams (Arnold et al. 1991). A relatively large surface area is more effective at generating negative lift than a small one (Webb 1975, 1978). This may explain why we observed that stream populations tended to have larger paired fins when compared with lake-dwelling populations. A number of past studies have also found that salmonid morphology is influenced by water velocity, but the morphological response to higher velocity can vary both within and between species. For example, Riddell and Leggett (1981) found that juvenile Atlantic salmon (*Salmo salar*) from a higher gradient stream differed than those from a lower gradient stream primarily in pectoral fin length and possibly as a result of higher water velocities in the high-gradient stream. Among individuals within populations, both McLaughlin and Grant (1994) and Imre et al. (2002) found that brook trout from high water velocities had larger caudal fins than those from lower water velocities, but they found opposing differences in caudal peduncle height. Similarly, Pakkasmaa and Piironen 2001 found that Atlantic

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salmon had deeper bodies under increased flow, but brown trout (*Salmo trutta*) exhibited no difference. Although past studies have consistently found that water velocity influences salmonid morphology, the variability in morphological responses suggests that other factors also play a role.

Within stream ecotypes, anadromous populations exhibited the most distinctive morphology. Anadromous populations tended to have the largest mouth and head size as well as the largest eye size among all rainbow trout populations. This distinctive morphology is associated with an ontogenetic habitat shift from a freshwater to a marine environment that is absent in both resident stream ecotypes. In addition to facing a prolonged period in a stream environment as juveniles, anadromous fish must undertake long migrations and cope with a switch to feeding on fish in an ocean environment (Pearcy 1992). Since our samples include fish taken prior to ocean migration (i.e., in an environment similar to that of resident fish), anadromous rainbow trout morphology may, therefore, reflect adaptation to this ontogenetic switch between freshwater and marine environments.

Rainbow trout from populations that were classified as piscivorous had some features that were larger in comparison with all other lake populations. As expected for a predator that feeds on relatively large prey, our prediction that piscivorous rainbow trout would have the largest mouth features among all lake populations was supported by relatively large premaxilla and head lengths. As in other taxa of fishes, species that tend to have a large proportion of fish in their diet also tend to have large mouths relative to their body size than nonpiscivorous species or populations (Snorrason et al. 1994; Wainwright and Richard 1995). In addition to mouth morphology, piscivorous rainbow trout appear to have a narrow caudal peduncle relative to other lake ecotypes. Although we know of no other intraspecific study with a similar result, others have noted that across fish taxa, open-water predators such as the billfishes (Xiphiidae) and tunas (Scombridae) do tend to have relatively narrow caudal peduncles, a trend that has been argued to stem from selection for the most efficient configuration for an open-water, cruising predator (Lindsey 1978; Webb 1978). The samples from the piscivorous populations that we studied also included juveniles collected from stream and littoral lake habitats prior to the initiation of open-water piscivory at about age 2 and 20 cm in length (Andrusak and Parkinson 1984). This suggests that the morphological differences that we found are not entirely induced by the unusual diet and habitat of adult piscivores.

The presence of competing species is a factor that is thought to be an important force in shaping the phenotype of a species. In fishes, numerous examples exist of dramatic trophic and morphological diversification among species that depends on the composition of competitors present in lakes (Robinson and Wilson 1994). We chose to compare lakes where rainbow trout had no fish competitors present, with lakes where only a benthos competitor, a plankton–benthos competitor, or both types were present. In salmonids, benthic catostomid species that feed on larval insects at the bottom of lakes are important competitors for this potential prey source for coexisting salmonids (Magnan 1988). In rainbow trout, cyprinid fishes such as redside shiners (*Richardsonius balteatus*) or lake chub (*Couesius plumbeus*) may be important plankton competitors (Johannes and Larkin 1961; Magnan 1988). We predicted that the presence of such species might be responsible for a displacement of morphological characters in rainbow trout because of this potential competitive influence. Our data indicate that rainbow trout from solitary populations tend to have some of the smallest head features of all of the populations that we sampled but were not significantly different from the populations that were sympatric with a minnow species. As Magnan (1988) and Bourke et al. (1999) suggested, small-bodied cyprinid or minnow species may actually impose very little competitive influence on co-occurring salmonids. The similarities in morphology among solitary rainbow trout populations and those that were sympatric only with a minnow species are consistent with this observation.

Despite the importance of gill raker length and spacing in exploiting zooplankton prey in some species of freshwater fish (e.g., Lavin and McPhail 1986; Sanderson et al. 2001), we could not detect any pattern of diversification in gill rakers among the lake populations of rainbow trout that we sampled. Intraspecific divergence in gill raker morphology is common in fish but was noticeably absent among the populations that we studied. Most previous observations are in sympatric benthic–pelagic species pairs (Taylor 1999) and appear to be the result of character displacement driven by competition (Pritchard and Schluter 2001). Sympatric populations of closely related species show similar character displacement (e.g., McDowell 1998). The absence of divergence that we observed among allopatric populations of rainbow trout that were paired with benthic and pelagic competitors suggests that distantly related species do not produce the same level of character displacement as closely related species or sympatric populations of the same species.

Unlike external features, internal organ sizes did not provide as strong discriminating abilities. For instance, despite living in a flowing-water environment, there appeared to be only a small difference between stream-dwelling populations and lake populations in terms of heart size. Given that ventricle size is correlated with cardiac output and aerobic capacity (Farrell et al. 1990), we expected that stream populations, which must swim continually to maintain position, would have a larger heart size than lake populations. Similarly, we also expected intestine size in piscivorous populations to be relatively small because piscivorous fishes tend to have a shorter gut length than omnivores or herbivores (Kramer and Bryant 1995). Instead, we found little difference among ecotypes, which suggests that gut size has not been influenced by differences across ecotypes.

Within ecotypes, morphological differences among individual fish from the same population were smaller than the differences among individuals from different populations. In contrast with our large-scale comparison, these differences cannot be replicated in different locations and there are no a priori predictions for the type of differences that may be expected. Nevertheless, these observations are consistent with the presence of adaptive radiation among populations within an ecotype. Previous studies of anadromous trout have documented differences among populations in life history characteristics, such as percentage of repeat spawning, time of

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return to fresh water, and adult body size (Withler 1966) along with the heritability of some of these differences (Smith 1969; Tipping 1991). The other ecotypes in this study have not been examined as extensively as anadromous trout, but we expect that the variation among the ecotypes that we observed is only a fraction of the overall variation among populations within this species.

A key goal of our work is to develop a practical method of documenting adaptive genetic variation to identify rare and endangered ecotypes for conservation purposes. Phenotypic variation among populations, such as that documented in this study, probably results from a combination of genetic divergence and phenotypic plasticity (Robinson and Parsons 2002). We did not estimate the heritability of each trait in each population, and therefore, we cannot differentiate genetic variation from phenotypic plasticity. However, if the association between environment and phenotype is partially the result of genetic adaptation to local environmental conditions, then the environment can be used as a surrogate for genetic variation. The success of this approach depends on the strength of this relationship between genetic and environmental variation.

Several lines of evidence suggest that the association between morphological and environmental variation that we observed in rainbow trout is partially the result of natural selection for genetically based traits that have adaptive significance. Clearly, some variation in morphology is the result of phenotypic plasticity (Pakkasmaa and Piironen 2001; Imre et al. 2002), but a variety of studies have shown that differences in morphology between salmonid populations have significant, measurable heritabilities (Riddell et al. 1981; Skúlason et al. 1989; Proulx and Magnan 2004). These differences occur in consistent, predictable directions (larger fins at higher velocity, larger mouths in piscivores), which suggests that some are likely under selective pressure in natural environments (Taylor 1991). More directly, we have obtained evidence of a genetic basis of the phenotypic difference that we have documented in this study for a subset of six populations representing solitary lake, mixed-species lake, piscivorous lake, headwater stream, large river, and anadromous ecotypes (E.R. Keeley, E.A. Parkinson, and E.B. Taylor, unpublished data). In this companion study, between 18% and 79% of the total phenotypic variation (depending on the trait) was attributable to differences among ecotypes raised under controlled environmental conditions (E.R. Keeley, E.A. Parkinson, and E.B. Taylor, unpublished data). Although we could not partition maternal effects from the among-population component of the variation, the persistence of ecotypic morphological differences under controlled environmental conditions supports the idea that much of the phenotypic variation that we have documented is under genetic control and can respond to different, environment-specific selection regimes. In our data set from the native populations, juveniles from at least two ecotypes (anadromous, piscivore) can be differentiated from other ecotypes prior to entering their distinctive environments. Distinguishing what proportion of the variation in morphology is a response to varying environmental conditions or represents relatively fixed differences as a result of selection remains to be tested experimentally in rainbow trout ecotypes.

Conservation implications of ecotypic variation

Intraspecific diversity has been recognized as an important component of biodiversity (Waples 1995; Waples et al. 2002) and is particularly important in areas such as the freshwater habitats of northwestern North America, which have a relatively depauperate fish fauna. British Columbia covers an area of approximately 950 000 km^2 but has fewer than 70 officially described species of native freshwater fishes. Taxonomic units in conservation plans clearly must include more than the species level of classification to capture adaptive divergence among populations within species (Hard 1995; Allendorf and Waples 1996; Crandall et al. 2000).

Diversity among rainbow trout populations has been an issue for biologists attempting to create lists of regional fauna for some time. Early efforts to describe rainbow trout diversity from British Columbia resulted in three described species: anadromous (steelhead) trout (*Salmo gairdneri*), Kamloops trout (*Salmo kamloops*), and mountain Kamloops trout (*Salmo kamloops whitehousei*), as well as earlier speculation on up to 16 different types of rainbow trout (Jordan et al. 1930; Dymond 1932; Mottley 1936*a*). Although early researchers recognized that different forms occupied different ecological roles, all forms of rainbow trout were eventually placed under a single species (*S. gairdneri* and later *O. mykiss*; Stearley 1993) because some of the meristic characteristics used to define a species were found to be largely environmentally induced (Mottley 1936*a*, 1936*b*). As is the case for neutral molecular diversity, some meristic characters may be used to define phylogenetic groups but may not represent ecological characteristics that are important for persistence in particular environments. Because our analysis has shown that significant morphological variation, under at least partial genetic control, is consistently associated with habitat characteristics that are relatively easy to quantify on a large scale, it may provide a practical methodology for conservation planners to encapsulate differences among populations of polytypic species that are of high conservation concern. In the face of ever-expanding threats to native populations by human activities, our method provides a precautionary means of assessing the frequency of relatively rare forms of rainbow trout before any damaging activities occur. This is an important consideration in conservation planning where priorities for protection must be assessed among thousands of populations that cannot be examined individually. For example, we were able to morphologically distinguish populations of large piscivorous rainbow trout from other populations. This ecotype is consistently found only in lakes greater than about 10 000 ha in surface area that also support kokanee (*Oncorhynchus nerka*), which is the key prey species for piscivorous rainbow trout in these lakes. Importantly, fewer than 15 lakes in British Columbia fit this description and those easily accessible to humans have had stringent harvest regulations imposed because of heavy exploitation pressure.

Habitat–phenotype associations that we have documented in rainbow trout suggest a landscape ecological approach that can be used as an alternative proxy measure of adaptive variation, i.e., inferring phenotype divergence from habitat (Watters et al. 2003). This approach, in combination with phylogeographic diversity (e.g., Crandall et al. 2000;

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McCusker et al. 2000) and landscape genetics (how landscape may influence gene flow among populations; e.g., Manel et al. 2003), can form an important component of assessing conservation priorities. Our study represents a contribution towards justification, when necessary, of a means to balance the desire for detailed scientific documentation of the adaptive significance of phenotypic variation among populations with the pragmatic need for conservation planning and decisions that must often be made over short time frames.

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Appendix A

Table A1. Location of sampling sites, ecotypic category, and fish species composition of water bodies used in morphological comparisons of rainbow trout (*Oncorhynchus mykiss*) populations.

Water body[a]	Population No.[b]	Ecotype	Fish species present[c]	Sample size	Longitude (°W)	Latitude (°N)
Thutade Lake	1	Mixed species 3	RB, KO, BT, MW, LSU, CC	18	126° 50.6′	56° 50.8′
Tatlatui Lake	2	Solitary	RB	50	127° 15.3′	56° 55.8′
Polley Lake	3	Mixed species 3	RB, LSU, RSC	50	121° 35.5′	52° 30.6′
Jacobie Lake	4	Mixed species 1	RB, LSU	50	121° 45.2′	52° 30.5′
Teeneiacut Lake	5	Mixed species 3	RB, LKC, LNC	50	122° 50.2′	52° 35.8′
Khtada Lake	6	Piscivore	RB, KO, DV	50	129° 25.5′	54° 05.5′
Ealue Lake	7	Solitary	RB	50	129° 50.0′	57° 45.3′
Canyon Creek	8	Headwater	RB, BT, CT	35	126° 45.6′	54° 40.7′
Division Lake	9	Mixed species 1	RB, LSU, CSU	50	125° 35.9′	54° 20.2′
Nellian Lake	10	Mixed species 3	RB, LSU, LKC	50	125° 40.8′	54° 20.6′
Hannay Lake	11	Mixed species 3	RB, LSU, WSU, LKC, BB	50	125° 00.3′	54° 15.6′
Kuyakuz Lake	12	Mixed species 3	RB, KO, LSU, LKC, MW, CA, NSC	50	124° 35.0′	53° 05.7′
Lucas Lake	13	Mixed species 3	RB, KO, LSU, WSU, LKC, MW, CA, NSC, BB	50	125° 10.0′	53° 30.7′
Moosevale Creek	14	Anadromous	RB, CH	35	126° 30.6′	56° 35.8′
Fry Creek	15	Headwater	RB	35	116° 45.7′	50° 00.6′
Bayonne Creek	16	Headwater	RB	35	116° 55.5′	49° 05.6′
Clearwater River	17	Large river	RB, CH	50	120° 10.2′	51° 55.0′
Coldwater River	18	Anadromous	RB, CH, CC	35	120° 50.6′	49° 45.7′
Nahmint River	19	Anadromous	RB, CO, CH	35	124° 55.5′	49° 05.2′
Memekay River	20	Anadromous	RB, CO, DV	35	124° 45.6′	50° 05.9′
Tsitika River	21	Anadromous	RB, CO, CH, CT, PL	35	126° 25.3′	50° 15.9′
Nimpkish River	22	Anadromous	RB, CO, CH	35	126° 35.1′	50° 10.3′
Gold River	23	Anadromous	RB, CO, CH	35	126° 05.1′	49° 50.2′
Heber River	24	Anadromous	RB, CO, CH	35	126° 00.2′	49° 45.5′
English Lake	25	Mixed species 2	RB, RSC, NSC	50	120° 35.8′	51° 30.9′
Fish Lake	26	Solitary	RB	50	123° 35.3′	51° 25.4′
Chaunigan Lake	27	Mixed species 2	RB, RSC	50	123° 55.7′	51° 30.8′
Blackwater River	28	Large river	RB, NSC, MW	50	123° 30.9′	53° 05.5′
Eutsuk Lake	29	Piscivore	RB, KO, MW, SU	80	126° 45.7′	53° 18.9′
Pennask Lake	30	Solitary	RB	50	120° 05.9′	49° 59.4′
Dean River	31	Large river	RB, SU, CB	50	125° 26.9′	52° 36.5′
Pimainus Lake	32	Solitary	RB	35	121° 04.5′	50° 24.3′
Murray Creek	33	Headwater	RB	35	121° 22.2′	50° 25.5′
Kootenay Lake	34	Piscivore	RB, KO, BT, SU	48	116° 51.5′	49° 36.3′
Blanchet Lake	35	Mixed species 3	RB, LNC, LKC	50	126° 18.0′	53° 24.2′
Small Lake	36	Mixed species 3	RB, LNC, LKC	50	126° 23.1′	53° 22.3′
Large Lake	37	Mixed species 3	RB, LNC, LKC	50	126° 25.3′	53° 21.2′
Thutilias Lake	38	Mixed species 3	RB, LSC, LNC, LKC	50	126° 14.4′	53° 24.5′
Grizzly Lake	39	Solitary	RB	50	126° 22.6′	53° 24.5′
Glatheli Lake	40	Mixed species 3	RB, MW, LNC, LSC, LKC	50	126° 20.1′	53° 38.2′
Unnmed Lake	41	Mixed species 3	RB, KO, MW, LSC, LNC, SQ, LKC	50	126° 28.3′	53° 37.0′

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Table A1 (*concluded*).

Water body[a]	Population No.[b]	Ecotype	Fish species present[c]	Sample size	Longitude (°W)	Latitude (°N)
Michel Lake	42	Mixed species 3	RB, LSC, LNC, KO, NSC, MW	50	126° 29.8′	53° 35.8′
Lake 43	43	Mixed species 3	RB, LNC, LKC	50	126° 20.2′	53° 36.6′
Kidney Lake	44	Solitary	RB	50	126° 19.4′	53° 36.9′
Ghitzeli Lake	45	Mixed species 3	RB, KO, LNC, LSC, NSC, LKC	50	126° 15.4′	53° 38.0′
Theleteban Lake	46	Mixed species 3	RB, KO, LNC, LSC, NSC	50	126° 13.1′	53° 35.3′
Fenton Lake	47	Mixed species 3	RB, LKC, LNC	50	126° 29.1′	53° 30.0′
Goodrich Lake	48	Mixed species 3	RB, LKC, LNC	50	126° 31.8′	53° 30.3′
Morgan Lake	49	Mixed species 3	RB, LKC, LNC	50	126° 19.9′	53° 30.0′
Nutli Lake	50	Mixed species 3	RB, LKC, LNC	50	126° 16.7′	53° 29.5′
Twinkle Lake	51	Mixed species 3	RB, LSC, LNC, NSC, MW, BT, CC	50	127° 01.1′	53° 48.5′
Needle Lake	52	Mixed species 3	RB, KO, SU	50	126° 58.4′	53° 48.9′
Lake Unamed	53	Mixed species 3	RB, SU, LKC	50	127° 06.3′	53° 48.2′
Upstream Lake	54	Mixed species 3	RB, SU, LKC	50	126° 55.9′	53° 48.2′
Skinny Lake	55	Mixed species 3	RB, KO, CA, LNC, LSC, MW, BB, NSC	50	126° 53.6′	53° 49.6′
Upstream Skinny Lake	56	Mixed species 3	RB, SU, LKC	50	126° 53.9′	53° 47.0′
Horseshoe Lake	57	Mixed species 3	RB, MW, KO, LNC, LSC	50	126° 50.4′	53° 50.4′
No Man Creek	58	Headwater	RB	50	126° 38.0′	53° 49.1′
Chelaslie River	59	Large river	RB	50	125° 55.1′	53° 28.7′
Star Lake	60	Mixed species 1	RB, SU	50	125° 52.7′	53° 31.0′
Unamed Creek	61	Headwater	RB	50	125° 52.6′	53° 27.4′

[a]Geographic place names are from Canadian topographic maps of British Columbia. If no official place name was available from the map, we assigned an unofficial place name.

[b]Refer to locations in Fig. 1.

[c]RB, rainbow trout (*Oncorhynchus mykiss*); KO, kokanee (*Oncorhynchus nerka*); LSC, largescale sucker (*Catostomus macrocheilus*); LNC, longnose sucker (*Catostomus catostomus*); LKC, lake chub (*Couesius plumbeus*); RSC, redside shiner (*Richardsonius balteatus*); BT, bull trout (*Salvelinus confluentus*); DV, Dolly Varden (*Salvelinus malma*); CO, coho salmon (*Oncorhynchus kisutch*); CH, chinook salmon (*Oncorhynchus tshawytscha*); CT, cutthroat trout (*Oncorhynchus clarki*); CA, prickly sculpin (*Cottus asper*); CB, mottled sculpin (*Cottus bairdi*); CC, unknown sculpin species (*Cottus* sp.); MW, mountain whitefish (*Prosopium williamsoni*); BB, burbot (*Lota lota*); SU, unknown sucker species (*Catostomus* spp.); NSC, northern squawfish (*Ptycheleilus oregonensis*); PL, Pacific lamprey (*Lampetra tridentata*).

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Fish use of stage-specific fluvial habitats as refuge patches during a flood in a low-gradient Illinois stream

John S. Schwartz and Edwin E. Herricks

Abstract: A stage-specific habitat classification scheme was developed emphasizing the ecological importance of habitat space as flow refugia for fish. Habitat units were based on planform and channel morphology and the resulting three-dimensional hydraulic patterns that form during floods. Fish were sampled in specific habitat patches using prepositioned areal electrofishing devices at two high-flow stages, near bankfull flow and one-half bankfull flow, during a flood. Fish were also sampled at baseflow immediately following the flood to compare changes in habitat use related to flow stage. During the bankfull stage, fish were found to use floodplain habitat units identified as vegetated point bars and concave-bank benches. During the one-half bank-full stage, fish density and biomass were greater in low-velocity habitat units identified as deflection eddies and expansion eddies than in the high-velocity habitat unit identified as the channel thalweg. Once flow returned to baseflow, fish density and biomass were greater in the main channel habitat units (pools, riffles, and glides) than in lateral habitat units identified as submerged point bars and lateral backwaters. This study provided a framework to quantify flow refugia in low-gradient streams, which is especially important in the restoration of anthropogenically disturbed watersheds that have lost habitat connectivity.

Résumé : Une méthode de classification des habitats en fonction des stades de la crue, que nous avons mise au point, met en relief l'importance écologique de l'habitat spatial comme refuge dans le courant pour les poissons. Les unités d'habitat sont basées sur la forme en plan et la morphologie du chenal et des patrons hydrauliques tridimensionnels résultants qui s'y forment durant les crues. Nous avons échantillonné les poissons dans des parcelles déterminées d'habitat à l'aide d'appareils prépositionnés de pêche électrique sur des surfaces déterminées, à deux stades de fort débit durant une crue, soit à un débit à pleins bords et à un débit représentant la moitié du débit à pleins bords. Nous avons aussi échantillonné les poissons à un débit de base immédiatement après la crue afin de comparer les changements d'utilisation de l'habitat en fonction du stade de la crue. Durant les débits à pleins bords, les poissons utilisent les unités d'habitat de la plaine de débordement, identifiés comme des barres de méandres couvertes de végétation et des replats des rives concaves. Au stade des débits correspondant à la moitié du débit à pleins bords, la densité et la biomasse des poissons sont plus grandes dans les habitats à courant réduit, identifiés comme des tourbillons de déflexion et des tourbillons d'expansion, que dans les unités d'habitat à fort courant, identifiés comme le thalweg du chenal. Une fois le débit retourné au niveau de base, la densité et la biomasse des poissons sont plus grandes dans les unités d'habitat du chenal principal (profonds, rapides et glissoires) que dans les unités latérales identifiées comme les barres de méandre submergées et les eaux dormantes latérales. Notre étude fournit un canevas pour quantifier les refuges contre le débit dans les coureau à pente faible; cela est particulièrement important pour la restauration des bassins versants perturbés par les humains et ayant perdu la connectivité entre leurs habitats.

[Traduit par la Rédaction]

Introduction

Resilience of fish assemblages to floods is dependent on physical habitat complexity that forms flow refugia (Lamberti et al. 1991; Pearsons et al. 1992). In small streams, more complex habitat structure can provide quality patches for fish to escape adverse high velocities that displace or injure them (Seegrist and Gard 1972; Harvey 1987; Kelsch 1994). In high-gradient streams, habitat complexity is associated with side channels and large woody debris, which are recognized as important salmonid refuge (Nickelson et al. 1992; Harvey et al. 1999). In large low-gradient streams, fish move into floodplains during prolonged spring flooding (Ross and Baker 1983; Kwak 1988), where fish life histories have

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J.S. Schwartz.[1] Department of Civil and Environmental Engineering, 63 Perkins Hall, University of Tennessee, Knoxville, TN 37996, USA.
E.E. Herricks. Department of Civil and Environmental Engineering, MC-250, University of Illinois, Urbana, IL 61801, USA.

[1]Corresponding author (e-mail: jschwart@utk.edu).

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evolved to exploit the rich food resources that this lateral habitat provides seasonally (Junk et al. 1989). In small upland streams, Poff and Allan (1995) suggested that fish have adapted to complex habitats and episodic flows. They found that fish assemblages were correlated with measures of daily discharge and flood frequency. It is apparent in streams that both refuge patch quality and highly variable flows play dominant roles as abiotic controls on fish community structure. However, the characteristics that distinguish habitat patches specifically as flow refugia for fish have not been adequately described in low-gradient streams.

During high-flow stages in low-gradient streams, stream habitat can no longer be characterized by traditional classification schemes that delineate habitat units as pools, riffles, and glides. Physically, the hydraulic environment changes as flow stage increases in a stream such that depth-averaged downstream velocities converge in greater magnitude at both pool and riffle positions (Keller and Florsheim 1993; Thompson et al. 1999). This fluvial process is known as the velocity-reversal hypothesis and underscores the view that pool and riffle habitats change between low- and high-flow stages. Flow patterns are more complex at high-flow than at low-flow stages in small streams. Flow patterns are three-dimensional affected by hydraulic resistance associated with all morphological surfaces, including channel bed and bank, floodplain platforms, and large in-channel structures. Knighton (1998) described flow as a high-velocity core that moves helically downstream through pool–riffle–bar morphology in both straight and meandering channels. In meanders, the high-velocity core is deflected by the point bar toward the outside bend and drops vertically down the pool entrance face (Dietrich 1987; Frothingham and Rhoads 2003). This topographic deflection results in convective acceleration of the flow at the pool entrance, causing lateral transfer of momentum and the formation of large-scale coherent eddies over the inner bank point bar. Large-scale eddies also occur where the channel width abruptly expands (Schmidt et al. 1993). With this channel morphology, flow is separated by a high-velocity core rapidly passing a laterally positioned water mass that forms a large eddy. In small low-gradient streams, bank vegetation strongly influences channel hydraulics forming low-velocity lateral areas (Nepf 1999; Rhoads et al. 2003). These fundamental fluvial principles are critical to developing a geomorphological and hydraulic framework for habitat classification of high-flow refuge patches. The main principles identified include the following: (*i*) the velocity reversal hypothesis, (*ii*) three-dimensional flow complexity depends on hydraulic resistance from boundary roughness of all morphological surfaces, and (*iii*) flow masses are separated by distinct hydraulic boundaries between the high-velocity core and lateral areas that can form large-scale eddies also termed hydraulic recirculation zones.

Characterization of flow refugia as habitat patches must scale to organism size and correlate with the relevant hydrodynamic phenomenon at that spatial scale (Schwartz 2002). For example, benthic macroinvertebrates seek refuge from high velocities in microhabitats of low velocity near the streambed (Statzner 1981; Osborne and Herricks 1987; Winterbottom et al. 1997), whereas fish must seek flow refugia in microhabitats of larger scale. The patch dynamic concept developed from these macroinvertebrate studies on flow refuge is essential to understanding stream ecosystems (Townsend 1989; Lancaster and Hildrew 1993; Negishi et al. 2002). However, the patch dynamic concept has not been well applied to fish habitat use associated with the dynamics of channel-scale hydraulic characteristics. This may be in part due to the difficulty of sampling fish during floods.

Fish refuge has typically been studied from a nonflood perspective and is generally described ecologically as feeding and resting sites associated with some type of cover. For example, in high-gradient streams, these sites commonly occur as velocity shelters behind physical structures such as large woody debris, root wads, and boulders (Fausch and White 1981; McMahon and Hartman 1989; Robison and Beschta 1990). In small low-gradient Illinois streams, large woody debris is not a dominant structural component of fish habitat; rather, habitat complexity consists of planform structures such as meanders and bars, floodplain sloughs from remnant channels, and concave-bank benches (Frothingham et al. 2002; Schwartz 2002). These planform structures create large low-velocity fluvial habitats where fish can gather during floods, such as hydraulic recirculation zones at meanders. To adequately characterize patterns of fish habitat use of flow refugia, we need habitat-specific sampling at flood stages.

The study objective was to characterize patterns of fish use among fluvial habitat units that represent flow refuge patches by using prepositioned areal electrofishing devices (PAEDs) to sample fish during a flood. Refuge patches for fish in small low-gradient Illinois streams were uniquely characterized by planform complexity and hydraulics at two high-flow stages. This habitat characterization scheme differs from other low-flow schemes that typically define mesohabitat units such as pools, riffles, and glides at baseflow stages (Arend 1999). In accomplishing this field study, fish use patterns during a flood event were characterized for high-flow fluvial habitat units, which are ecologically relevant as flow refugia.

Methods

Study area

The research site was located on a third-order stream in the upper Embarras River basin approximately 15 km south of Urbana, Illinois. Regionally, Pleistocene glaciation created a gently sloping landscape forming a low-gradient basin with channel gradients approximately 0.075%. Upstream of the research site, the 476-km^2 basin area primarily drains agricultural lands hydromodified from channelization and the use of drain tiles. The research site included a 1-km reach of the upper Embarras River in mostly undisturbed meandering channel, except for drain tile discharges (Fig. 1). Native and exotic grasses cover floodplains and stream banks (Fig. 2). Stream flows range from 0.15 $m^3 \cdot s^{-1}$ during summer dry periods to approximately 12 $m^3 \cdot s^{-1}$ at the near bankfull stage (Frothingham 2000). During this study, stream water temperatures ranged diurnally between 16.8 and 21.8 °C.

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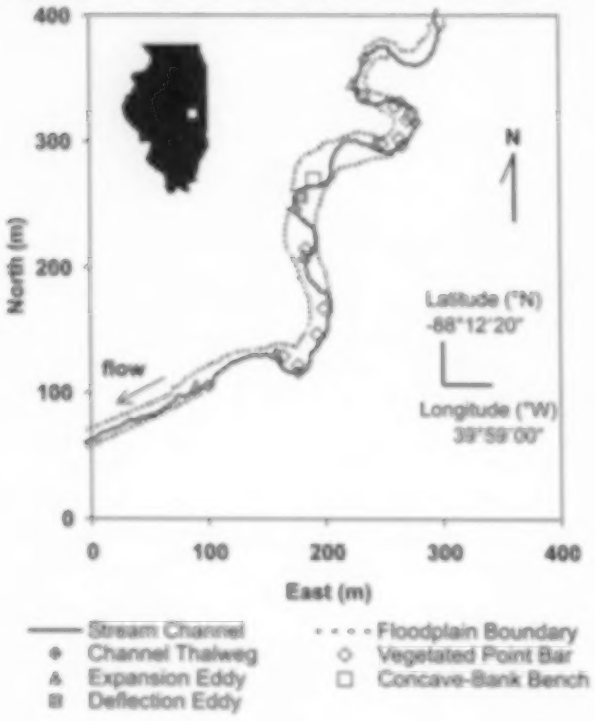
Fig. 1. Spatial distribution of fish sample locations on the upper Embarras River, Champaign County, Illinois (inset), USA.



Study design

Fluvial habitat units were delineated at two distinct high-flow stages based on three-dimensional hydrodynamics in which large-scale hydraulic patterns are governed by reach planform and channel morphology (Table 1). The distinct flow stages were (*i*) a stage contained within the main channel but not overflowing onto higher elevation floodplain platforms and (*ii*) a stage inundating floodplain platforms (Fig. 3). In this high-flow habitat classification scheme, fluvial habitat units included the channel thalweg as a single unit representing the high-velocity corridor and low-velocity lateral patches at the two high-flow stages (Fig. 2). In the main channel at both flow stages, lateral habitat patches included a deflection eddy unit and an expansion eddy unit and a corridor unit that consisted of channel margins with thick grassy-vegetation forming hydraulic dead zones. Lateral habitat patches that occur only during inundation of floodplain platforms included a vegetated point bar unit, a concave-bank bench unit, and a remnant channel unit. A third stage was sampled at baseflow but only to compare fish habitat use patterns between high- and low-flow stages. At baseflow, habitat units were designated as a pool, riffle, glide, lateral backwater, and submerged point bar as defined by Arend (1999) and Schwartz (2002).

Fish were sampled during a single flood event on 6 and 7 June 2001 and on 11 June 2001 when the stream returned to baseflow for comparison (Fig. 3). The rainfall event that generated this flood totaled 5.36 cm between 4 and 6 June 2001 (Illinois State Water Survey Weather Station 119740, Urbana, Illinois). Sample sites for each flow stage were selected along the 1-km study reach moving upstream during the field day, delineating habitat unit boundaries using the criteria set forth in Table 1. These units were flagged with survey stakes to relocate them at a later date and surveyed with a total station referenced to a research site datum consisting of a permanent survey monument. Immediately following each site fish sampling, physical habitat was measured as average water depth, depth-averaged velocity over the PAEDs using a Global Flow Probe (model FP201; Global Water Instrumentation, Inc., Gold River, California), and, if relevant to stage, eddy surface area measured as an areal estimate of length and width.

On 6 June 2001 when the flow stage was near bankfull flow at approximately 12 $m^3 \cdot s^{-1}$, fish were sampled in inundated habitat units on floodplain platforms, including nine vegetated point bars and a concave-bank bench (Fig. 1). On this day, the channel thalweg unit was not sampled because depth and velocity precluded safe and effective sampling. On 7 June 2001 when the stage receded to approximately one-half bankfull at approximately 5 $m^3 \cdot s^{-1}$, fish were sampled in habitat units of the main channel. At this stage, the current remained swift in the channel thalweg unit and hydraulic recirculation zones formed at sharp-bended meanders (deflection eddy units) and rapid expansions of the channel width (expansions eddy units). Samples included seven locations along the corridor of the channel thalweg unit and eight lateral channel locations consisting of deflection eddy and expansion eddy units (Fig. 1).

On 11 June 2001, when a baseflow stage returned at approximately 0.7 $m^3 \cdot s^{-1}$, fluvial habitat units in the main channel were sampled for fish, but in this case, the units were based on low-flow habitat criteria. Between high and low flows, fluvial habitat units are spatially related in the channel position. These stage-dependent habitat relationships included the following: (*i*) the channel thalweg unit at high flow consisted either of a pool, riffle, or glide units at baseflow, (*ii*) an expansion eddy unit consisted of a lateral backwater unit at baseflow, and (*iii*) a deflection eddy unit at a meander consisted of a submerged point bar unit at baseflow. Lateral eddy locations remained similar between flow stages in that they formed an eddy delineated by separated flow and differentiated by their morphological characteristics (Schwartz 2002). Sampling fish between stages at one-half bankfull flow and baseflow supported the study design for a two-factor comparison between flow stage and habitat unit type.

Habitat-specific fish collection

Fish were sampled with PAEDs designed with different-length rod electrodes to sample specific habitat volumes of varying dimensions (Schwartz and Herricks 2004). PAED placement data were recorded so that fish immobilization distance from the electrodes could be estimated and used to compute the exact sample volume. Data recorded at each sample location included electrode lengths, orientation to each other (parallel or serial), distance between electrodes, and voltage output. Immobilization range is also affected by water conductivity (Reynolds 1996); therefore, specific conduc-

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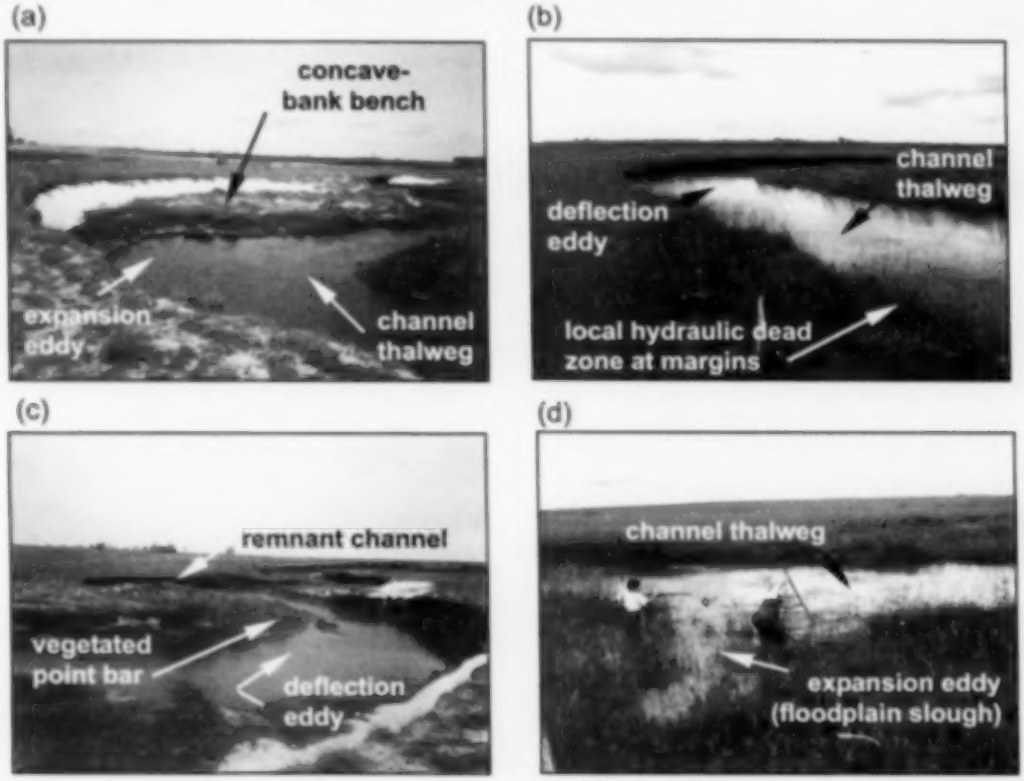
Fig. 2. Fluvial habitat units on the upper Embarras River, Illinois, showing (*a*) an expansion eddy at a concave-bank bench and the channel thalweg, (*b*) a deflection eddy at a meander and the local hydraulic dead zone at vegetated margins, (*c*) a remnant channel and vegetated point bar platform, and (*d*) an expansion eddy at a floodplain slough.



tance was measured daily using a Chemtrix type 700 conductivity meter (Chemtrix, Hillsboro, Oregon). Accuracy of the conductivity meter was confirmed with a laboratory-grade 400 $\mu S \cdot cm^{-1}$ standard solution.

PAED electrode sets were placed in designated habitat units, defined by the classification scheme in Table 1, along the study reach starting at the downstream end and working upstream. A PAED electrode set included wire extending to a nonflooded bank area to connect a 2.0-kW generator–transformer power source and activate the electrodes for fish sampling (Schwartz and Herricks 2004). Fish were sampled without fright bias because the electrodes were left undisturbed for a minimum period of 15 min before activation. Upstream, most electrodes were typically left undisturbed for several hours. Once the PAED electrodes were activated from the bankside power source, two or three netters entered the stream from the bank to capture immobilized fish in the designated habitat unit. Immobilized fish in the low-velocity habitat units could be captured by dip netters. In the high-velocity channel thalweg unit, an 8-mm-mesh block net was placed approximately 10 m downstream of a PAED set in a manner that net placement minimized fish fright, and PAEDs were activated after a 15-min wait. Immobilized fish captured were measured for standard length to the nearest millimetre and weighed with an Ohaus scale (model CS2000; Ohaus Corporation, Pine Brook, New Jersey). Fish were released to their captured location, except for a few individuals retained for species identification verification and a reference collection.

Data analysis

Fish data for each sample corresponding to flow stage and habitat unit type were summarized into fish density (fish per square metre) and biomass (grams per square metre). Summary statistics on fish measurements for each habitat unit type included an average and a coefficient of variation. For this study, young-of-the-year (YOY) fish were designated as less than 1 g and 35 mm in total length for all families expect Centrarchidae. Centrarchidae YOY were designated as less than 3 g and less than 45 mm in total length.

A two-way contingency table was used to test whether the sampled fish assemblages differed among flow stage using Pearson's χ^2 statistic and it was completed in a computer spreadsheet (Legendre and Legendre 1998). Fish assemblage per each flow stage was summarized as percent species abundance and total number of species observations per habitat unit sample (Table 2). The null hypothesis represented statistical population homogeneity in which the fish species collected at each flow stage were similar. The null hypothesis, if accepted, infers that the sampling effort captured the same reach-scale community structure at different flow stages. It is assumed that the fish species only dispersed dif-

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Table 1. Geomorphic and hydraulic characteristics of high-flow fluvial habitat units at two flow stages above baseflow in small low-gradient streams.

Fluvial habitat unit type	Geomorphological characteristics	Hydraulic characteristics	Selected references
Flow stages above baseflow inundating lateral transition areas between the main channel and floodplain platforms			
Channel thalweg	Lowest bed elevation in active channel; path of maximum depth and velocity within the channel; often shifts laterally across channel in conjunction with pool–riffle–bar morphology	Convergent–divergent flow pattern associated with pool–riffle–bar morphology; strong downstream velocities; helical flow in pools	Dietrich 1987; Knighton 1998; Frothingham and Rhoads 2003
Deflection eddy	Intermediate bed elevation at margin of main channel along point bar face and vegetated platform; wetted inundation above baseflow; strong topographic deflection of flow laterally by elevated point-bar head, especially in sharp bends, resulting in an elongated zone of flow separation along inner bank	Separated, recirculating flow	Bagnold 1960; Dietrich 1987; Frothingham and Rhoads 2003
Expansion eddy	Intermediate bed elevation within main channel laterally; wetted inundation above baseflow; abrupt expansions of channel width at local reentrants associated with remnant channels (floodplain sloughs); early stages of concave-bank bench development in meandering channels; local bank ledge failures or other large structures that create local lateral channel constrictions	Separated, recirculating flow within expansion zone	Page and Nanson 1982; Howard 1992; Schmidt et al. 1993
Local hydraulic dead zone at margins	Channel margins adjacent to thalweg in straight and meandering channels with high hydraulic roughness consisting of local bank irregularities and dense vegetation; wetted inundation above baseflow	Stagnant or low-velocity areas produced by high hydraulic roughness	Nepf 1999; Rhoads et al. 2003
Flow stages above one-half bankfull flow inundating floodplain platforms			
Vegetated point bar	Elevated floodplain platform above main channel; inundated at bankfull or overbank flows; grassy vegetated zones on surface of point bar platform along inner (convex) bank of meander bends	Near zero velocities or recirculating flow produced by high hydraulic roughness during bankfull flow	Nanson and Croke 1992; Knighton 1998
Concave-bank bench	Elevated surface above main channel; flood inundation only during bankfull or overbank flows; crescent-shaped depositional area at location corresponding to upstream limb of concave bank in the next bend downstream; bench typically vegetated with grass	Separated, recirculating flow resulting from enlargement of expansion eddy during bankfull flow	Page and Nanson 1982; Nanson and Croke 1992
Remnant channels, mouth of floodplain slough	Elevated surface above main channel; flood inundation only during bankfull or overbank flows; remnant channels lateral to active channel; gradually slope towards reentrants locations at the mouth of floodplain sloughs	Separated, recirculating flow resulting from enlargement of expansion eddy during bankfull flow	Howard 1992; Nanson and Croke 1992

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Fig. 3. Channel transect at a meander on the upper Embarras River, Illinois, illustrating the sampled flow stages associated with the high-flow fluvial habitat classification scheme and basedflow. Elevation and transect distance are relative to the study site datum.

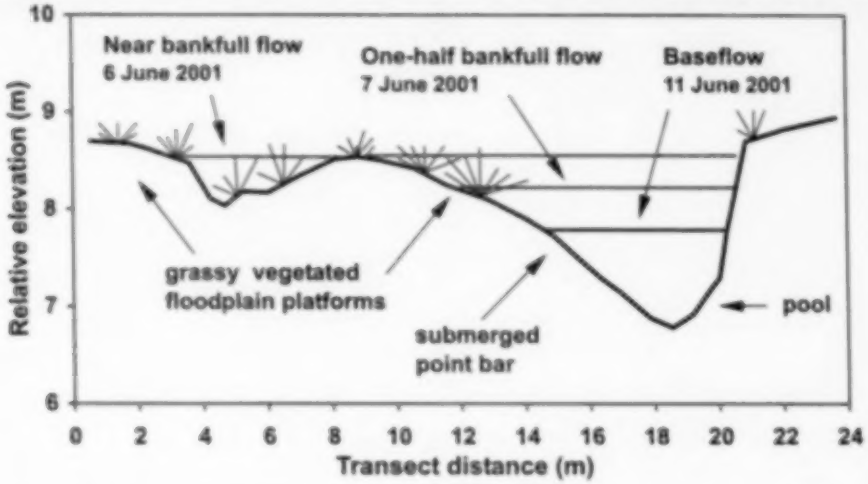

Table 2. Summary of fish species captured on 6, 7, and 11 June 2001 in the upper Embarras River, Illinois, as percent abundance per sampled flow stage with the number of observations per sample habitat unit per flow event in parentheses.

	% abundance		
Species	Near bankfull flow	One-half bankfull flow	Baseflow
Bluntnose minnow (*Pimephales notatus*)	36.7 (9)	44.0 (13)	25.3 (14)
Sand shiner (*Notropis ludibundus*)	21.5 (9)	10.4 (10)	27.3 (9)
Central stoneroller (*Campostoma pullum*)	8.6 (5)	8.2 (7)	5.2 (11)
Creek chub (*Semotilus atromaculatus*)	3.5 (5)	4.9 (3)	11.2 (11)
Redfin shiner (*Lythrurus umbratilis*)	5.9 (6)	2.6 (3)	9.9 (9)
Longear sunfish (*Lepomis megalotis*)	4.3 (6)	6.7 (12)	5.0 (8)
Silverjaw minnow (*Notropis buccatus*)	6.3 (4)	7.1 (10)	1.2 (4)
Johnny darter (*Etheostoma nigrum*)	5.9 (6)	3.7 (5)	3.2 (8)
Blackstripe topminnow (*Fundulus notatus*)	1.2 (3)	3.7 (7)	6.2 (9)
Steelcolor shiner (*Cyprinella whipplei*)	3.1 (5)	1.9 (5)	2.2 (5)
Striped shiner (*Luxilus chrysocephalus*)	2.0 (3)	1.1 (3)	0.7 (2)
Green sunfish (*Lepomis cyanellus*)	0.4 (1)	3.0 (4)	0.2 (1)
Brindled madtom (*Noturus miurus*)	0.0 (0)	1.9 (1)	0.7 (3)
Golden redhorse (*Moxostoma erythrurum*)	0.4 (1)	0.0 (0)	0.2 (1)
Yellow bullhead (*Ameiurs natalis*)	0.0 (0)	0.4 (1)	0.2 (1)
Golden shiner (*Notemigonus crysoleucas*)	0.4 (1)	0.0 (0)	0.0 (0)
Common carp (*Cyprinus carpio*)	0.0 (0)	0.4 (1)	0.0 (0)
Greenside darter (*Etheostoma blennioides*)	0.0 (0)	0.0 (0)	0.2 (1)
Pirate perch (*Aphredoderus sayanus*)	0.0 (0)	0.0 (0)	0.2 (1)
Rainbow darter (*Etheostoma caeruleum*)	0.0 (0)	0.0 (0)	0.2 (1)
Suckermouth minnow (*Phenacobius mirabilis*)	0.0 (0)	0.0 (0)	0.2 (1)
Total fish abundance	256	268	403
Total number of habitat units sampled	10	15	15

ferently among habitat units as per flow stage designated uniquely by the proposed classification scheme. The observation frequency consisted of species presence per sampled habitat unit. This observation for the two categories (species and flow stage) was used because abundance or other measures induce bias based on species traits; for example, schooling species may be collected in much larger numbers than solitary species. In addition as recommended by Legendre and Legendre (1998), fish species with a small number of observations were not used so that the expected frequency values were always greater than 1.

A two-sample independent *t* test was used to test mean differences in fish and physical habitat metrics among habitat unit types per flow stage (SPSS version 10.0; SPSS Inc.,

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Table 3. Fish and physical habitat measurements per habitat unit sampled on 6 June 2001 at near-bankfull flow, upper Embarras River, Illinois.

Habitat unit type	Fish density (fish·m^{-2})	% YOY fish	Average water depth (m)	Unit sample area (m^2)
VPB	1.32	13.3	0.74	11.4
VPB	4.65	28.3	0.62	11.4
VPB	2.89	57.6	0.76	11.4
VPB	0.88	0.0	0.47	11.4
VPB	0.35	0.0	0.55	11.4
VPB	3.77	16.4	0.33	14.6
VPB	0.79	50.0	0.54	15.2
VPB	0.66	60.0	1.06	15.2
VPB	4.24	8.9	0.41	10.6
CBB	1.06	52.6	0.42	18.3
Average	2.06	28.7	0.59	
CV	80.3	84.3		

Note: Habitat unit type designated as vegetated point bar (VPB) and concave-bank bench (CBB); YOY, young-of-the-year; CV, coefficient of variation.

Chicago, Illinois). Statistical assumptions for parametric procedures were checked using the Kolmogorov–Smirnov test for normality and the Levene test for equality of variances. For the one-half bankfull flow stage, fish and physical habitat metrics were compared between channel thalweg units and (*i*) deflection and expansion eddies combined and termed "eddy" habitat units and (*ii*) deflection eddies and expansion eddies separately. Simple linear regression models were also used to explore relationships between fish densities in eddy habitat units at the one-half bankfull stage and various eddy habitat metrics (eddy surface area, length to width ratio, and water depth). For the baseflow stage, fish and physical habitat metrics were compared between pool–riffle–glide units combined and (*i*) lateral backwater and submerged point bar units combined as lateral habitat and (*ii*) lateral backwater and submerged point bar units separately.

A two-way analysis of variance was used to examine the interaction between the two factors flow stage and habitat unit types for fish and physical habitat metrics. In addition, a paired-sampled *t* test was used to test mean differences in fish data between one-half bankfull flow and baseflow stages among paired habitat unit types consisting of (*i*) channel thalweg – pool–riffle–glide units, (*ii*) expansion eddy – lateral backwater units, and (*iii*) deflection eddy – submerged point bar units.

Results

Fish assemblages among flow stages

Fish assemblages sampled per flow stage, consisting of near bankfull flow, half-bankfull flow, and baseflow, were statistically similar based on a contingency table analysis of fish species occurrence per sampled habitat unit (Table 2) (df = 24, $p = 0.64$). Similarity of fish assemblages among flow stages suggested that the sampling effort captured most of the common species typically found in the study reach at the flow stages sampled. In addition, this result suggested that water turbidity and specific conductivity that differed during flow stage did not greatly affect sampling performance. Water was turbid during the flood period and cleared slightly at the baseflow stage. Specific conductivities were measured at 400 μS·cm^{-1} on 6 June 2001, 600 μS·cm^{-1} on 7 June 2001, and 675 μS·cm^{-1} on 11 June 2001.

Fish habitat use and physical habitat characteristics: near bankfull flow stage

During near bankfull flow, fish densities ranged between 0.35 and 4.65 fish·m^{-2} for 10 habitat units consisting of vegetated point bars and a concave-bank bench (Table 3). Fish density averaged 2.06 fish·m^{-2} in these habitat units and was four times greater than the average of 0.47 fish·m^{-2} found in channel thalweg units the following day. These results, together with the fact that fish assemblage structure did not change among flow stages, strongly suggest that fish dominantly used these floodplain platform areas as flow refuge. Percent YOY fish among these habitat units averaged 28.7% and ranged between 0.0% and 60.0%. All habitat units at this flow stage had submerged and emergent grassy vegetation. Water depths ranged between 0.33 and 1.06 m, and velocities were measured as approximately zero.

Fish habitat use and physical habitat characteristics: one-half bankfull flow stage

During one-half bankfull flow, fish densities and biomass were greater in low-velocity habitat units (deflection and expansion eddies) than in the higher velocity channel thalweg units (Table 4). When data from deflection and expansion eddies were combined together as eddy habitat units and compared with channel thalweg units, fish density averaged 1.96 fish·m^{-2} in eddy habitat units and was four times greater than average fish density in the channel thalweg ($p = 0.015$). Similarly, average fish biomass was significantly greater in eddy units than in the channel thalweg ($p = 0.011$), where eddy units averaged 4.18 g·m^{-2} and the channel thalweg averaged 1.32 g·m^{-2}. Average biomass in the eddy units excluded a single 495-g common carp (*Cyprinus carpio*) collected from a deflection eddy because it created extremely high variance precluding reasonable statistical comparisons. With the single carp included, fish biomass in eddy

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Table 4. Fish and physical habitat measurements per habitat unit sampled on 7 June 2001 at one-half bankfull flow, upper Embarras River, Illinois.

Unit No.	Habitat unit type	Fish density (fish·m^{-2})	Fish biomass (g·m^{-2})	% YOY fish	Flow velocity (m·s^{-1})	Water depth (m)	Eddy area (m^2)	Eddy length to width ratio
1	CT	0.88	2.24	50.0	1.39	0.82	—	—
2	CT	0.18	0.39	50.0	0.74	0.82	—	—
3	CT	0.09	0.26	0.0	0.56	0.88	—	—
4	CT	0.35	1.23	25.0	1.12	0.85	—	—
5	CT	0.59	1.32	44.4	0.74	1.22	—	—
6	CT	0.53	1.36	33.3	0.74	0.82	—	—
7	CT	0.70	2.41	12.5	1.49	0.85	—	—
8	EE	0.50	1.40	40.0	0.00	0.67	6.0	2.70
9	EE	1.34	3.63	26.1	0.08	0.55	13.0	3.25
10	EE	0.93	2.92	29.4	0.00	0.70	32.0	2.00
11	EE	1.64	2.35	56.7	0.00	0.79	18.0	2.00
12	EE	1.23	2.54	21.4	0.03	0.82	6.0	2.70
13	DE	2.14	5.79*	36.7	0.04	0.52	24.0	2.70
14	DE	3.79	7.86	49.1	0.00	0.43	16.0	4.00
15	DE	4.07	6.96	43.9	0.00	0.61	16.0	4.00

Note: Habitat unit type designated as channel thalweg (CT), expansion eddy (EE), and deflection eddy (DE). YOY, young-of-the-year.
*Shown without the single 495-g common carp; if included, fish biomass for the habitat unit is 41.14 g·m^{-2}.

Table 5. Fish and physical habitat measurements per habitat unit sampled on 11 June 2001 at baseflow, upper Embarras River, Illinois.

Unit No.	High-flow unit location	Low-flow habitat unit type	Fish density (fish·m^{-2})	Fish biomass (g·m^{-2})	% YOY fish	Flow velocity (m·s^{-1})	Water depth (m)
1	CT	R	2.02	10.48	26.1	0.28	0.52
2	CT	R	4.12	14.74	8.5	0.60	0.56
3	CT	G	3.51	10.70	10.0	0.21	0.58
4	CT	R	5.18	13.20	5.1	0.60	0.52
5	CT	P	1.97	24.70	10.0	0.16	0.98
6	CT	G	1.32	8.95	13.3	0.19	0.52
7	CT	R	2.89	5.31	3.0	0.63	0.55
8	EE	LB	1.50	4.05	40.0	0.00	0.34
9	EE	LB	0.58	0.55	50.0	0.00	0.27
10	EE	LB	1.48	4.62	14.8	0.00	0.46
11	EE	LB	1.09	2.46	20.0	0.00	0.43
12	EE	LB	1.05	3.60	8.3	0.00	0.55
13	DE	SPB	1.71	1.79	16.7	0.00	0.26
14	DE	SPB	2.07	1.29	10.3	0.00	0.26
15	DE	SPB	1.36	2.07	10.5	0.00	0.44

Note: Habitat unit types designated at one-half bankfull flow location as channel thalweg (CT), expansion eddy (EE), and deflection eddy (DE), and in addition to low-flow habitat designations as riffle (R), glide (G), pool (P), lateral backwater (LB), and submerged point bar (SPB). YOY, young-of-the-year.

units averaged 8.60 g·m^{-2}. Percent YOY fish was similar between eddy and channel thalweg units ($p = 0.397$) in which averages for these habitat unit types ranged between 30.7% and 43.2%. Physical habitat between eddy and channel thalweg units was clearly distinguished by average downstream velocity and water depth (Table 4). Velocity in the channel thalweg units averaged 0.97 m·s^{-1} and was significantly greater than an average of 0.02 m·s^{-1} in the eddy units ($p = 0.019$). In addition, average water depth in channel thalweg units was 0.89 m and was greater than the average of 0.64 m for eddy units ($p = 0.003$).

When data from deflection and expansion eddies were compared separately with channel thalweg units, fish densities were significantly greater in deflection and expansion eddy units than channel thalweg units ($p = 0.038$ and 0.010, respectively). Similarly, fish biomasses were significantly greater in deflection and expansion eddy units than in channel thalweg units ($p \leq 0.001$ and 0.026, respectively).

Fish density and biomass in deflection eddies were greater than in expansion eddies ($p = 0.055$ and 0.001, respectively). Fish metrics averaged 3.33 and 6.87 g·m^{-2} in the deflection eddies compared with 1.13 and 2.57 g·m^{-2} in the expansion eddies (Table 4). Average biomass in deflection eddy units was 18.65 g·m^{-2} when the single large carp was included in the estimate. Percent YOY fish was not statistically different between deflection and expansion eddy units ($p = 0.370$). Water depth and the eddy length to width ratio were the only physical measures that differed between the deflection and expansion eddies ($p = 0.003$ and 0.060, respectively). Average water depth was 0.52 m in the deflection eddies, which

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was shallower than 0.71 m, the average water depth in the expansion eddies. Deflection eddies were more narrow than expansion eddies, with average length to width ratios of 3.57 and 2.53, respectively. Fish densities correlated directly with eddy length to width ratio (R^2 = 0.64, p = 0.017) but were less correlated with water depth (R^2 = 0.32, p = 0.144). Velocity and total eddy surface area were similar between these eddy habitat types (p = 0.719 and 0.605, respectively).

Fish habitat use and physical habitat characteristics: baseflow stage

When the flow stage returned to baseflow, fish density and biomass were greater in pool–riffle–glide units than in lateral backwater and submerged point bar units (Table 5). Fish density averaged 3.00 fish·m^{-2} in the pool–riffle–glide units and was significantly greater than an average fish density of 1.36 fish·m^{-2} in lateral backwater and submerged point bar units (p = 0.018). When analyzed separately, fish density was greater in the pool–riffle–glide units than in the lateral backwaters (p = 0.010) and submerged point bars (p = 0.051). Fish biomass averaged 12.58 g·m^{-2} in the pool–riffle–glide units and was also significantly greater than an average biomass of 2.55 g·m^{-2} in lateral backwater and submerged point bar units (p = 0.005). When analyzed separately, fish biomass was significantly greater in the pool–riffle–glide units than in the lateral backwater units (p = 0.006) and submerged point bars (p = 0.003). Percent YOY fish in the lateral backwater units was twice that found in the pool–riffle–glide units and submerged point bar units (p = 0.118 and 0.150, respectively). Velocity averaged 0.38 m·s^{-1} in the pool–riffle–glide units and was significantly greater than the near zero average velocity in the lateral backwater and submerged point bar units (p = 0.008). Water depths in the pool–riffle–glide units ranged from 0.52 to 0.98 m and averaged 0.41 m for lateral backwater units and 0.32 m for submerged point bar units. Average water depth in lateral backwater and submerged point bar units was significantly less than in pool–riffle–glide units (p = 0.007).

Changes in fish habitat use: one-half bankfull to baseflow flow stages

Patterns of fish habitat use were strongly influenced by flow stage (Table 6). During one-half bankfull flow, fish dominantly used eddy habitat (deflection and expansion) units over the channel thalweg units (Fig. 4). This pattern was reversed 4 days later during the baseflow stage when fish dominantly used the main channel pool–riffle–glide units compared with lateral habitats (lateral backwater and submerged point bar units). Statistical interaction between the two factors flow stage and habitat unit type was observed for fish density, fish biomass, and average downstream velocity (p < 0.001, <0.001, and 0.028, respectively). In the deflection and expansion eddy units, fish biomass averages were significantly different between flow stages (p = 0.021 and 0.046, respectively), but fish densities were not found to be different (p = 0.134 and 0.973, respectively). Percent YOY fish was strongly influenced by flow stage, but no interaction was found with habitat unit type (p = 0.299). Percent YOY fish differed among stage-defined habitat between channel thalweg and pool–riffle–glide units and deflection

Table 6. Statistical summary of fish density, biomass, and percent juvenile fish for habitat unit types at the one-half bankfull and baseflow stages including habitat unit average and coefficient of variation (CV), and paired-sample t test for each habitat unit type between flow stages, upper Embarras River, Illinois.

		Fish density (fish·m^{-2})			Fish biomass (g·m^{-2})			% YOY fish		
Habitat unit comparison	Flow stage	Average	CV	p	Average	CV	p	Average	CV	p
Channel thalweg: pool, riffle, and glide units	One-half bankfull	0.47	59.7	0.005	1.32	62.3	0.004	30.7	62.9	0.020
	Baseflow	3.00	45.4		12.58	48.8		10.9	69.3	
Expansion eddy: lateral backwater units	One-half bankfull	1.13	38.4	0.973	2.57	31.8	0.046	34.7	40.5	0.461
	Baseflow	1.14	33.1		3.06	52.7		26.6	66.3	
Deflection eddy: submerged point bar units	One-half bankfull	3.33	32.6	0.134	6.87*	15.1	0.021	43.2	14.4	0.032
	Baseflow	1.71	20.7		1.72	23.0		12.5	29.1	

Note: YOY, young-of-the-year.
*Shown without the single 495-g common carp; if included, fish biomass average is 18.65 g·m^{-2} and CV = 104.4.

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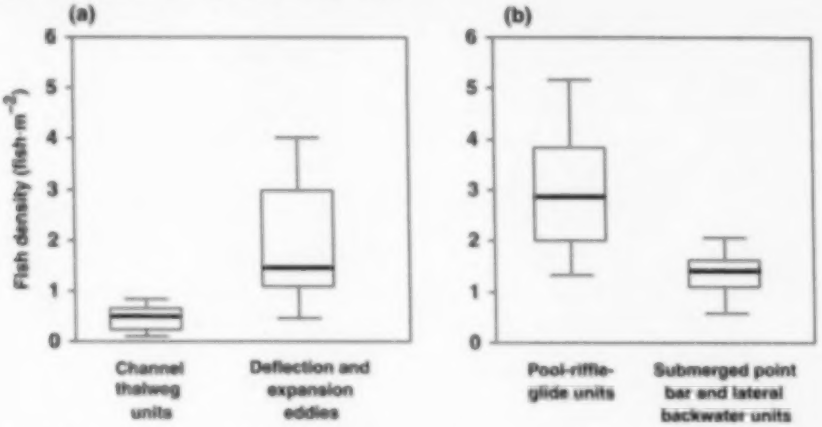
Fig. 4. Fish densities summarized for fluvial habitat units on the upper Embarras River, Illinois, at the same fish sample sites but differing by (*a*) the one-half bankfull flow and (*b*) the baseflow stage.



eddy and submerged point bar units but not between expansion eddy and lateral backwater units.

The dominant physical difference between these flow stages was velocity, indicated not only by the differences in the average downstream velocity in the channel thalweg but also by the presence of large-scale eddies in the lateral channel areas (Tables 4 and 5). Channel thalweg velocities ranged between 0.56 and 1.49 $m \cdot s^{-1}$ during the one-half bankfull flow stage and between 0.16 and 0.83 $m \cdot s^{-1}$ during the baseflow stage ($p = 0.004$).

Discussion

In small low-gradient streams, traditional habitat classification schemes do not account for changes in ecological function of habitat space from low- to high-flow stages. Traditionally, mesohabitats are classified as pool, riffle, and glide, where habitat unit designations rely solely on streambed morphology observed at low-flow stages and a one-dimensional perspective of hydraulics (Hawkins et al. 1993; Arend 1999). We argue that pools, riffles, and glides are only ecologically relevant and physically identifiable at low-flow stages. Supporting this argument, Rowntree and Wadson (1996), when applying traditional habitat classification schemes as flow stage rises, found that a greater proportion of the longitudinal length of mesohabitat becomes a glide. Fish distributions are known to change with habitat structure altered by hydraulics at varying flow stages (Schlosser 1985; Aadland 1993). However, most patterns of fish habitat use among mesohabitat units are well documented only at low-flow stages (Gelwick 1990; Rabeni and Jacobson 1993; Hayes and Jowett 1994). Advancements in hydrodynamic modeling in recent years have provided some new insights into defining the multidimensional character of hydraulic habitat (Crowder and Diplas 2000), but ecological function of habitat remains founded in a low-flow stage perspective that includes feeding and resting sites. This study exemplifies that stage-specific characterization of fish habitat units is critical to quantify high-flow refugia, another important ecological function of fish habitat.

Previous flood-related studies, in their focus on the importance of low-velocity refuge areas to fish survival, have relied on fish sampling in only low-flow conditions (Harrell 1978; Matthews 1986; Lobón-Cerviá 1996). These studies focused only on general measures of habitat complexity and were not able to connect fish use and flow refugia. By applying PAED technology and special field protocols to sample fish during floods, we were able to develop habitat-specific relationships with refuge habitat structure (Schwartz and Herricks 2004). Fish use of hydraulic recirculation zones, visually observed as large-scale lateral eddies, can be described by three-dimensional hydraulics and sampled separately from the flood high-velocity corridor following the channel thalweg.

This study illustrates the importance of incorporating three-dimensional hydraulics into the characterization of flow refugia for fish. For example, at one-half bankfull flow stage, we found that fish density and biomass were greater in deflection eddies than in expansion eddies. Larger fish tended to occupy the deflection eddies located at sharp meanders, as observed by the higher biomass average for this habitat unit type. Of the physical metrics, water depth and the eddy length to width ratio were the only metrics that significantly differed between the deflection and expansion eddy units. Velocity and eddy surface area were not significant. Deflection eddies tended to be shallower and narrower than expansion eddies. These findings suggested that the larger fish may sense some hydraulic characteristic other than a simple, average velocity. In other words, flow refuge was simply not a low-velocity area. We speculate that fish sense closeness to the vertical shear layer separating the high-velocity core from the hydraulic recirculation zone or possibility a turbulence structure that fish perceive as safe. Some studies suggest that turbulence structure is important for salmonid behavioral selection of habitat and guidance of downstream migrating juveniles (Coutant 2001).

The question of whether turbulence guides fish to safe areas was explored using field measurements of three-dimensional velocity data by Frothingham (2000) at two fish sample sites on the Embarras River but collected 4 years earlier. These data were used to compute average turbulence

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kinetic energy for a deflection eddy and an expansion eddy at one-half bankfull flow. Average turbulence kinetic energy for the defection eddy was computed as 52.3 $cm^2 \cdot s^{-2}$ and was greater than the 20.0 $cm^2 \cdot s^{-2}$ computed for an expansion eddy (J.S. Schwartz, unpublished data). These findings suggest that fish may specifically key in on hydraulic conditions, but further research is needed to confirm that habitat selection behavior is associated with turbulence structure.

Although larger fish more often were found in deflection eddies than in expansion eddies for flow refuge at one-half bankfull flow, YOY fish did not appear to be selective of these units. Expansion eddies, which have submerged and emergent grass during high flows, provided good flow refuge for smaller fish. This supports Dewey's (1992) observations that habitat with submerged and emergent grass supports good fish nursery areas. This grass on the floodplain platform extends to the edge of lateral backwater units and provides good bank cover for small fish during baseflow. Percent YOY fish in lateral backwater units was twice that in submerged point bar units. The morphological complexity associated with expansion eddies and lateral backwater habitat units is important for small fish rearing in low-gradient streams.

Bank margins, commonly vegetated with overhanging grass in small Illinois stream, also form a local hydraulic dead zone during intermediate flood stages. Although bank margins were one of the basic fluvial habitat unit types for high flows, our experimentation focused on fish use of hydraulic recirculation zones. However, the importance of bank margin habitat units cannot be overlooked. Of the fish captured in the channel thalweg units at one-half bankfull flow, 30.7% were YOY fish, of which 22.5% were longear sunfish (*Lepomis megalotis*). Longear sunfish have a morphology and musculature not conducive for maintaining position in fast water. In addition, of the channel thalweg units at one-half bankfull flow, fish densities were greatest in two channel thalweg units that were heavily vegetated on both banks (0.70 and 0.88 fish·m^{-2}). A likely explanation for this finding is that fish in the vegetated margins sensed the PAED electrical field and initiated an ocillotaxis response darting into the main flow. They became immobilized after being swept downstream through the electrical field into our block net. If this is true, comparisons between channel thalweg and eddy habitat units were conservative because some fish captured in the channel thalweg units likely came from vegetative bank margins rather than thalweg positions. Further study of marginal habitats using this study's PAED technique would improve knowledge of what species and life stages require this flow refuge patch.

Characterization of flow refugia by definable fluvial habitat units, as done in this study, provides a means to link different habitat units to specific fish species and life stage requirements and thereby quantify the loss of ecological connectivity along a stream corridor. This is particularly important in agricultural regions of the midwestern United States where many streams continue to be channelized, eliminating meandering and other complex planform and channel morphologies (Rhoads and Herricks 1996). Loss of longitudinal and lateral connectivity from anthropogenic impacts that fragment refuge habitat is a major ecological concern (Sedell et al. 1990; Rosenburg et al. 1997; Ward et al. 2001). The mesohabitat classification scheme developed for this study provides a means to quantify loss of this connectivity through field surveys of reach flow refugia. Importantly, the scheme links habitat space of low-flow habitat at the pool–riffle scale with high-flow refuge at the reach scale, recognizing that channel morphology and habitat are maintained during high-flow discharges. This geomorphological and three-dimensional hydraulics framework of flow refugia can be useful in the ecological design of stream restoration projects. Schwartz (2004) applied a two-dimensional hydrodynamic model to a test case illustrating how information from this study can be applied to stream restoration design. While this study has better defined flow refugia for fish in low-gradient streams, broader scale research is needed to quantify what level of refugia fragmentation initiates degradation of fish community structure in anthropogenically disturbed watersheds.

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A bioeconomic analysis of management strategies for rebuilding and maintenance of the NSS rock lobster (*Jasus edwardsii*) stock in southern New Zealand

Daniel S. Holland, Nokome Bentley, and Philippe Lallemand

Abstract: We evaluated alternative management strategies for the Otago and Southland rock lobster (*Jasus edwardsii*) fisheries in New Zealand. We compare a number of decision-rule-based management strategies and assess amalgamation of the two separate quota management areas that currently comprise the fishery. The analysis combines a spatial sex- and length-structured simulation model of the fishery with an economic module that converts catches and effort into revenues and costs. We compare performance of alternative management strategies using a variety of biological and economic performance indicators relevant to a range of management objectives identified by stakeholders. The results demonstrate the importance of modelling economic performance, since the relative performance of different management strategies differ when considering catch versus net revenues. The analysis also reveals important distributional issues, since some strategies that increase the overall value of the fishery create both winners and losers.

Résumé : Nous avons évalué des stratégies alternatives pour la gestion de la pêche commerciale des langoustes (*Jasus edwardsii*) dans les régions d'Otago et de Southland en Nouvelle Zélande. Nous comparons un certain nombre de stratégies de gestion basées sur différentes règles d'aide à la décision tout en évaluant l'intégration possible des deux régions gérant les quotas et composant aujourd'hui cette pêche commerciale. Notre analyse combine un modèle de simulation de la pêche basé sur des données biologiques structuré en fonction du sexe et de la taille des langoustes et du lieu de la prise avec un module économique qui convertit les captures et efforts de pêches en revenus et coûts. Nous comparons la performance de stratégies de gestion alternatives à l'aide d'un éventail d'indicateurs de performance biologiques et économiques appropriés basés sur des objectives de gestion identifiés par les acteurs concernés. Les résultats obtenus démontrent l'importance de pouvoir modéliser la performance économique, puisque la performance relative des différentes stratégies de gestion varie en fonction que l'on considère soit les captures ou les revenues nets. Notre analyse révèle également d'importants problèmes distributionnels, car celles des strategies qui accroissent la valeur de la pêche commerciale affectée engendrent aussi bien des gagnants que des perdants.

[Traduit par la Rédaction]

Introduction

The NSS (North-South Island – South; Otago and Southland) rock lobster (*Jasus edwardsii*) stock has been managed with individual transferable quotas (ITQs) as part of the New Zealand quota management system (QMS) since 1990. The stock is divided into two quota management areas (QMAs): the Otago–CRA7 QMA and the Southland–CRA8 QMA (Fig. 1). The two QMAs have separate total allowable commercial catches, seasons, and minimum legal size. However, they are treated as a single stock for assessment purposes, primarily because of irregular migrations of immature animals from CRA7 to CRA8 (Street 1973, 1995; Kendrick and Bentley 2003). In the 2002–2003 fishing year, catches from the CRA7 and CRA8 areas were around 89 and 567 tonnes (t), respectively, with a combined exvessel value (value of green weight of fish landed) in excess of NZ$20 million. Like most lobster fisheries in New Zealand, the great majority of the catch is exported live, primarily to markets in Asia.

Rebuilding the NSS stock to safer and more productive levels has been a long-standing management goal. Upon introduction into the QMS, total allowable commercial catches (TACCs) for the two QMAs were set well below average catch levels in prior years and were subsequently reduced further. In the mid-1990s, catch rates were still low relative to historical levels, and it was determined that an increased stock size could likely support higher sustainable catches (Breen and Kendrick 1998; Starr and Bentley 2002).

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D.S. Holland[1] **and P. Lallemand.**[2] New Zealand Seafood Industry Council, Private Bag 24-901, Wellington, New Zealand.
N. Bentley. Trophia, P.O. Box 60, Kaikoura, New Zealand.

[1]Present address: Gulf of Maine Research Institute, 350 Commercial Street, Portland, ME 04101, USA (e-mail: dholland@gmri.org).
[2]Corresponding author (e-mail: lallemandp@seafood.co.nz).

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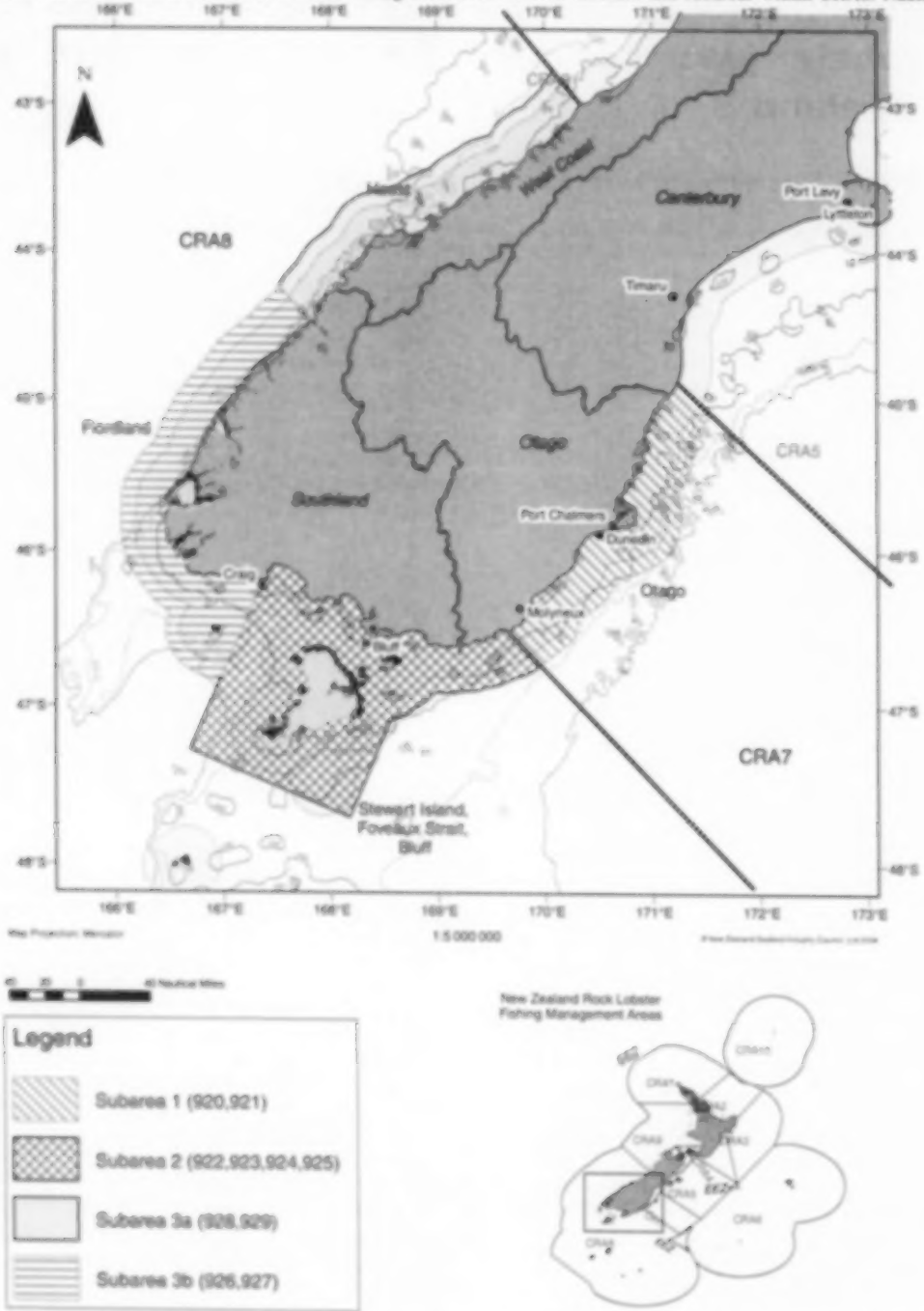
Fig. 1. CRA7 and CRA8 rock lobster (*Jasus edwardsii*) management areas in New Zealand and subareas within CRA8. Nautical miles, nmi.



In the mid-1990s, the National Rock Lobster Management Group (NRLMG), which advises the Minister of Fisheries on rock lobster management issues, began to explore decision rules for management. Decision rules use an agreed indicator, or set of indicators, from the fishery and specify what action will be taken, depending on the indicators. Under this approach, also called the management procedure approach (e.g., Butterworth and Punt 1999), prior agreement is obtained between managers and stakeholders about the indicator data, the decision rule, and the period for which the

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rule will be used. Loosely based on Germont et al. (1999), the advantages of this approach over the traditional pattern of regular or periodic stock assessments, each followed by a decision process, are as follows: harvest decision rules that are robust to uncertainty can be developed, the process leads to explicit definition of management objectives, all participants in the fishery can become involved in the choice of rule, a long-term view is forced, management procedures move away from regular assessments, thereby freeing resources for other research, and the process is more understandable to fishers than the traditional approach.

In 1997, a management procedure was adopted with a decision rule that was based on standardized catch per unit effort (CPUE) from the commercial fishery (CRA7 and CRA8 combined) as an index of abundance and acted on the TACCs for both QMAs in concert (Starr et al. 1997). Standardization of CPUE accounts for changes in the spatial and temporal distribution of effort (Bentley, Starr, and Hendrick, unpublished data). The rule caused reductions in the TACC in 1999 and again in 2001. The NRLMG explored refinements of management procedures for this stock and incorporated new information from a stock assessment in 2001 to evaluate the decision rule. This led to implementation of a new revised management procedure in 2002. The new procedure set a lower CPUE target for rebuilding and utilizes a revised decision rule that was found to adhere to the rebuilding trajectory with less variation in the TACC. Currently, a single-harvest decision rule based on CPUE in Southland triggers changes in the TACCs for both areas. The current decision rule was designed to achieve a CPUE-based rebuilding target by 2014 (Fig. 2).

The NSS stock appears to be rebuilding, and managers and stakeholders are interested in exploring further refinements to the management procedure to make it more suitable for maintenance of the fishery once it is rebuilt. Furthermore, the current decision rule's use of only Southland CPUE as an indicator was considered to be a temporary measure subject to future review. A simulation model was developed to assess both the biological and economic effects of alternative management strategies relative to the current one. Possible changes to the management procedure include alternative CPUE targets, as well as an alternative decision rule for adjusting the TACC over time that is expected to be more effective at maintaining CPUE (and presumably the vulnerable biomass) at the target level. The simulations also explore alternative stock management structures. We compare the current management structure with joint management with a decision rule using a weighted-average CPUE from both areas to adjust TACCs in both areas. We consider separate management of the two QMAs allowing the TACC in CRA7 to be adjusted in-season in response to CPUE during the season. Finally, we consider amalgamation of the two QMAs into a single area with consistent size limits and seasons in both areas.

The modelling is meant to provide stakeholders and managers with information that will enable them to consider tradeoffs among multiple management objectives that may be conflicting. In 2000, a workshop of stakeholders and the NRLMG agreed upon six primary management objectives (Bentley et al. 2003*a*, 2003*b*): maximize catch, maintain high abundance, minimize frequency of catch adjustments, minimize risk of low biomass levels, maximize the rate of rebuilding, and maintain a wide size-range of lobster. The performance indicators associated with each management objective provides a way of assessing trade-offs and choosing the optimum management strategy. However, there are clearly conflicts and trade-offs among these objectives. For example, some management strategies may achieve lower average yields but maintain higher average CPUE, which means lower costs. Some strategies may provide better long-term performance at the expense of lower catches or profits in the short run. Stakeholders often find it difficult to put explicit, quantitative weights on multiple performance indicators (Bentley et al. 2003*b*). This study provides a partial solution to this problem by using an economic model that implicitly weights some of the important performance indicators. The simulations done in this study include an economic submodel that calculates revenues, costs and net revenues. Different temporal patterns in the realization of cost and benefits can be evaluated by discounting long-term gains relative to those that accrue more quickly. Thus, we can monetize some trade-offs and rank management strategies according to objective criteria, such as the present value of the stream of cumulative net revenues. Trade-offs between higher average catches or net revenues and higher variation in catches or higher risk of stock depletions are more difficult to evaluate objectively with a single metric. Therefore, we still provide a variety of performance indicators relating to these objectives that stakeholders can use along with projections of profitability in their decision making process. The economic results of the model also help to fulfil increasing requirements for socioeconomic analysis to support fishery management decisions in New Zealand.

Methods

We combine a spatial, size- and sex-structured biological model with an economic submodel that transforms projections of catches and CPUE into revenue, effort, and costs. The structure and parameterization of the biological model are based on the 2000 NSS stock assessment (Bentley et al. 2001) and address the uncertainty associated with the assessment by sampling sets of parameters from the joint posterior distribution of the fully Bayesian assessment and allowing for stochastic variation in other uncertain parameters and processes. The economic model is based on price and harvest cost data provided directly by processors and fishers, respectively. We utilize this model to project biological and economic outcomes for a variety of alternative management strategies. The models produce information on a variety of indicators relating to the productivity, profitability, and risks of the management strategies.

Biological operating model

To preserve the readability of the paper, we provide only a brief description of the biological model here and describe the structure and parameterization of the model in more detail in Appendix A. Three distinct lobster populations and fisheries are simulated, representing Otago, Stewart Island – Foveaux Strait, and Fiordland. Although the latter two areas are both part of the CRA8 management area, we modelled Stewart Island – Foveaux Strait separately from Fiordland

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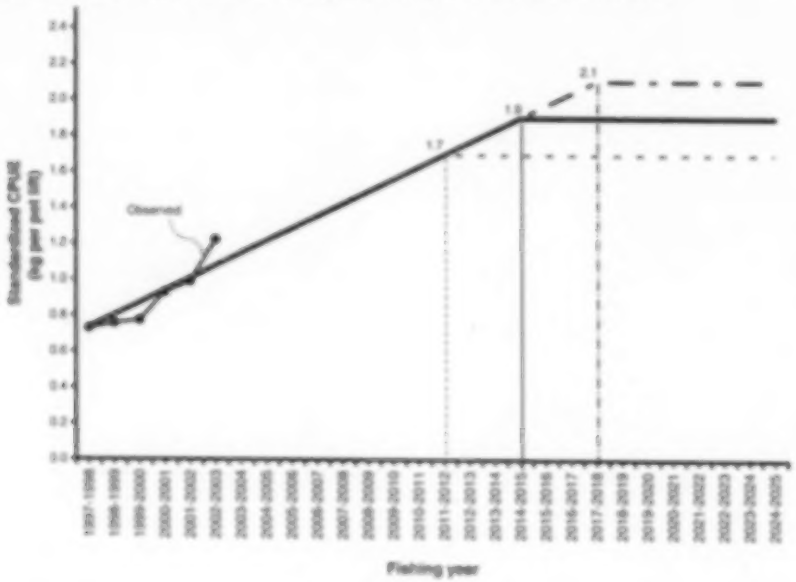
Fig. 2. The target biomass trajectory for CRA8 is generated by plotting a straight line from the observed starting value in the 1997–1998 fishing year to the target CPUE achieved in 2014–2015. Observed CPUE is generated from the standardized CPUE analysis for CRA8. For joint-stock management, both the targets and trajectory are scaled downward proportionately from what is shown in this figure to reflect the effect that CRA7 CPUE has on the weighted average CPUE for the two areas.



because the two areas have possibly different population dynamics and relationships with Otago. The model incorporated the minimum legal size (MLS), selectivity-, and maturity-at size characteristics of each of the three areas. The model operates on a semiannual time step with an autumn–winter (AW) season followed by a spring–summer (SS) season. A unidirectional migration pattern is modelled with lobster moving from Otago to Steward Island or Fiordland and from Stewart Island to Fiordland. Migration occurs at the start of the SS season. Recruitment to the three areas is also dependent on spawning stock biomass in the other areas (Appendix A).

The outputs of the biological model are CPUE and catch by commercial grade (which is weight based) for each of the three areas. The proportion of the annual TACC that is taken in each season (AW and SS) is specified in the model. The model calculates the breakdown of catches for each of nine commercial weight grades (Table 1) based on the relative abundance of lobster of each grade. The seasonal and grade-wise breakdown of catch is important, since prices for different grades differ substantially and prices tend to be considerably higher in the AW season than in the SS season.

Economic model

An economic submodel uses catch and CPUE from the biological submodel to calculate revenues and costs. We calculate total revenues and total costs separately for each of four fleets for each year of the simulation. We model one fleet (Otago) for CRA7 and three fleets (Stewart Island, Fiordland, and Haast) for CRA8. Although the biological model produces only a combined catch and CPUE for Fiordland and Haast, we model the fleets separately since their characteristics are quite different. Haast, like Otago, has mostly smaller vessels that make single-day trips, while vessels in Fiordland tend to be larger and stay out for long periods, with catches being delivered to processors periodically by helicopter. Although in this paper, we focus primarily on combined net revenues for the CRA7 and CRA8 fleets, modelling fleet-specific revenues and costs provides useful information for different groups of stakeholders and enables us to explore the economic consequences of shifts of catch between areas.

Table 1. Definition of commercial weight grades used in simulations and prices per kilogram for each grade in the AW and SS seasons.

		Prices per kg (NZ$)			
		CRA7		CRA8	
Grade	Weight range (kg)	AW	SS	AW	SS
AAA	0–0.3	30.45	29.88	NA	NA
AAMinus	0.3–0.4	31.58	30.36	42.53	30.19
AAPlus	0.4–0.5	31.90	29.81	42.34	30.16
A	0.5–0.6	31.85	29.62	43.69	32.25
B	0.6–0.8	36.31	32.68	43.73	28.95
C	0.8–1	40.50	33.22	48.11	32.07
D	1–1.5	38.55	34.01	47.65	32.73
E	1.5–2	29.03	30.33	42.87	28.65
Z	> 2.0	18.83	20.22	35.59	25.15

Note: NA, not applicable because the weight range is below legal size in CRA8.

Revenues

Processors provided monthly average prices for each management area and commercial grade during the 2001–2002 season. Since the simulations predict only seasonal rather

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than monthly catches, we calculated a weighted average seasonal price for each grade (Table 1). Prices remain constant over time in the simulations. While this is unrealistic, we do not have sufficient information to model prices. Changes in prices are primarily a function of exchange rates and conditions in Asian markets, to which most of the lobster are exported. Prices are not expected to be affected by the level of landings, since exports from CRA7 and CRA8 make up only a small percentage of the total volume of the markets they are sold into.

The annual revenue is calculated for each of four fleets based on catch projections from the simulations. The annual gross revenue R for fleet f in period t is calculated as

$$(1) \qquad R_{ft} = \sum_{s=1}^{2}\sum_{g=1}^{9} p_{fgs} q_{fgst}$$

where p_{fgs} is a price that is fleet (f), grade (g), and season (s) specific, q_{fgst} is the f-, g-, and s-specific landed catch weight in period t, s indexes two seasons (AW and SS), and g indexes nine weight-based grades.

Effort and fleet size

To calculate the total cost for each fleet, we need to determine the total level of effort for each fleet. The biological model projects a combined catch for the Fiordland and Haast fleets, which the economic submodel allocates between the two fleets according to the relative proportion of catch taken in the two areas in the 2001–2002 fishing year to get the total weight of catch Q_{fst} for each fleet area f, season s, and year t.

The biological model also projects a corresponding CPUE_{st} for each area–year. This must then be calibrated to account for differentials between observed average CPUE for the fleet in question relative to the observed CPUE of the vessels used to develop the cost model. The calibrated CPUE for each fleet (CPUE_{ft}) is calculated as

$$(2) \qquad \mathrm{CPUE}_{ft} = \frac{\mathrm{CPUE}_{st}}{\alpha_f}$$

where α_f is the ratio of the CPUE of the representative vessel used to model costs to the average CPUE for the area in the 2001–2002 fishing year (the year for which cost data were collected). The calibration for the individual vessels is done for the year rather than each season since catch and effort data by season were not available.

$$(3) \qquad \alpha_f = \frac{\mathrm{CPUE}_{a2001}}{\mathrm{CPUE}_{f2002}}$$

From this we can calculate total effort in terms of potlifts for each fleet based on seasonal catch as

$$(4) \qquad E_{ft} = \frac{\sum_{s=1}^{2} Q_{fst}}{\mathrm{CPUE}_{ft}}$$

We determine the number of vessels in each fleet N_f by assuming the annual level of effort per boat e_f remains constant and the fleet size expands or contracts as the TACC and CPUE change. Since CPUE tends to increase proportionately more than the TACC, the fleet size tends to decrease. The only effect this assumption has on cost calculations is on fixed costs, which are proportional to fleet size. Variable costs are proportional to total effort and are unaffected by assumptions about fleet size. If, contrary to our assumption, the fleet size remained constant and individual effort decreased, we might tend to underestimate fixed costs. However, in that case, it is likely that these vessels would shift effort into other fisheries that could defray some of their fixed costs. The number of vessels is calculated as

$$(5) \qquad N_{ft} = \frac{E_{ft}}{e_f}$$

Harvest costs

Since we assume a constant level of nominal fishing effort in terms of potlifts and days fished and adjust fleet size to account for changes in total effort, we can calculate a combined variable and fixed cost for each vessel in each fleet c_f that remains constant over time. We can then calculate total costs for each fleet C_{ft} as follows:

$$(6) \qquad C_{ft} = N_{ft} c_f$$

Total vessel cost (Table 2) for each of the four fleets incorporates variable costs for our assumed level of annual lobster fishing activity for that fleet along with fixed operating costs and an opportunity cost of capital equal to 10% off the market value of the fishing vessel and other capital assets. This can be represented as

$$(7) \qquad c_f = (\text{total variable cost per pot lift} \times \text{annual pot lifts per boat}) + (\text{crew wages} \times \text{hours fished}) + \text{fixed operating cost} + \text{capital cost}$$

Costs other than labour are derived from a survey of vessel operators in both CRA7 and CRA8. The survey was voluntary and was completed for ten vessels in CRA8 and five vessels in CRA7, which represents approximately 20% of the fleet in each area. The results showed significant differences in cost structure and efficiency across these vessels. Rather than use the survey data to calculate average costs and CPUE, with the help of stakeholder leaders we identified representative vessels for each of the four fleets and used their actual costs and CPUE to model costs and calibrate CPUE as described above. Since this was a somewhat subjective decision, we undertook a sensitivity analysis of

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Table 2. Summary of effort, cost, and revenue data collected from the survey of CRA7 and CRA8 fishers. For the main simulations, we use the annual effort level and costs of a typical vessel from each fleet, rather than the average costs and effort for the fleet.

	CRA7				CRA8			
	Whole region		Stewart Island, Foveaux Straight, Bluff		Haast		Fiordland	
Economic indicators	Typical vessel	Region average	Typical vessel	Region average	Typical vessel	Region average	Typical vessel	Region average
Days fished per year		120		80		61		95
Annual pot lifts	16 900	14 280	7 055	5 840	12 160	7 930	18 750	13 395
CPUE (kg·pot lift^{-1})		0.59		1.37		0.70		0.90
Region CPUE / Vessel CPUE		0.78		0.98		1.24		0.96
Price (NZ$)		32		35		35		35
Catch (kg)		8 425		8 001		5 551		12 056
Revenue (NZ$)	352 000	269 606	343 000	280 028	420 000	194 285	630 000	421 943
Variable cost (NZ$)		35 700		48 472		28 548		89 747
Crew wages + accident insurance (NZ$)		45 027		48 053		30 339		57 062
Fixed cost (NZ$)		16 000		24 000		8 500		31 500
Estimated capital cost (NZ$)		19 000		33 000		14 000		38 000
Total cost (NZ$)	159 619	115 727	180 313	153 525	141 588	81 387	248 494	216 309
Net revenues (NZ$)	192 381	153 879	162 687	126 503	278 412	112 898	381 506	205 634
Net revenues·kg^{-1} (NZ$)	17	18	17	16	23	20	21	17

the model using average harvest costs for each fleet, but found it made little difference in terms of the relative performance of management strategies.

Although labour is actually paid as a crew share, we model labour costs as a wage based on hourly wages estimates from 2002 New Zealand labour market statistics (Statistics New Zealand 2002). Thus, labour costs represent an opportunity cost of labour rather than a cash outlay. We use a wage rather than a crew share because many skippers are owner-operators and their actual crew share is simply the net profit. Also, shares of revenues for crew are likely to change over time if revenue per unit effort changes.

Net revenues and value of quota

We subtract total costs from total revenues for each year and fleet to calculate net revenues. Because the temporal distribution of benefits may differ across management strategies, we calculated the present value of net revenues (PVNR) as

$$\text{PVNR} = \sum_{t=1}^{21} \sum_{f=1}^{4} \frac{R_{tf} - C_{tf}}{(1+r)^t} \tag{8}$$

where r is the discount rate. We use a discount rate of 8% to calculate NPV. This is roughly equal to the real yield on long-term commercial bonds in New Zealand in 2003. The simulations run for 20 years from 2003 to 2022, so $t = 1$ in 2003 and $t = 20$ in 2022.

To calculate the benefits that accrue to stakeholders in the two different QMAs, we calculate the value of one t of quota (VTQ) for each QMA. We simply divide the PVNR for each QMA by the tonne of quota outstanding in 2003, the first year of the simulation:

$$\text{VTQ}_{\text{CRA7}} = \sum_{t=1}^{20} \frac{R_{t1} - C_{t1}}{(1+r)^t} \times \frac{1}{\text{TACC}_{\text{CRA7,2003}}} \tag{9a}$$

$$\text{VTQ}_{\text{CRA8}} = \sum_{t=1}^{20} \sum_{f=2}^{4} \frac{R_{tf} - \text{TC}_{tf}}{(1+r)^t} \times \frac{1}{\text{TACC}_{\text{CRA8,2003}}} \tag{9b}$$

where TC_{tf} is the annual total cost for fleet f.

For amalgamation, the calculation is slightly more complex, since amalgamation is not assumed to occur until 2005. VTQ is the sum of the PVNRs for each area for 2003–2004, and a proportional share of the combined PVNRs for 2005–2022:

$$\text{VTQ}_{\text{CRA7amalgamated}} = \left[\sum_{t=1}^{2} \frac{R_{t1} - C_{t1}}{(1+r)^t} \cdot \frac{1}{\text{TACC}_{\text{CRA7,2003}}}\right] + \left[\sum_{t=3}^{20} \sum_{f=1}^{4} \frac{R_{tf} - C_{tf}}{(1+r)^t} \cdot \frac{\text{TACC}_{\text{CRA7,2003}}}{\text{TACC}_{\text{CRA7+CRA8,2003}}}\right] \tag{10a}$$

$$\text{VTQ}_{\text{CRA8amalgamated}} = \left[\sum_{t=1}^{2} \sum_{f=2}^{4} \frac{R_{tf} - C_{tf}}{(1+r)^t} \cdot \frac{1}{\text{TACC}_{\text{CRA8,2003}}}\right] + \left[\sum_{t=3}^{20} \sum_{f=1}^{4} \frac{R_{tf} - C_{tf}}{(1+r)^t} \cdot \frac{\text{TACC}_{\text{CRA7,2003}}}{\text{TACC}_{\text{CRA7+CRA8,2003}}}\right] \tag{10b}$$

Evaluation methods

We simulate catches, revenues, and operating costs over a 20-year period beginning in 2003 for a variety of management strategies. The 20-year duration of the simulations was chosen by stakeholder representatives who commissioned the study. We compare current management to a number of

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alternative management strategies with different stock structures, decision rules for adjusting TACCs, and target CPUE levels. Any change to a new stock management structure is assumed to take place in 2005. This was the earliest point that a change in management would be feasible. For each stock management structure we consider three CPUE targets: the current target, targets 10% higher, and targets 10% lower. Changes to an alternative decision rule occur only once rebuilding to the CPUE target is complete.

The evaluation procedure addresses realism and uncertainty by incorporating uncertainty with respect to parameter values and the current state of the stock, uncertainty about interactions of the three substocks in CRA7 and CRA8, error in the use of CPUE as an index of vulnerable biomass, and the unpredictability of future recruitment. For each scenario modelled, a parameter set was sampled from the joint posterior distribution of parameters obtained in Markov chain Monte Carlo simulations from the 2000 stock assessment. We used 1000-sample parameter sets to initialize the model and simulated each management scenario for each sample. In each of the runs, stochastic process and observation error were simulated, and a random state-of-nature was obtained with respect to the stock-recruit dynamics and migration with specified ranges or distributions of process error, observation error, state-of-nature distributions, and projection errors (Table A1). Random recruitment variation was based on the mean of the 10 most recent recruitment deviations from the assessment. The model shuttles through all of the policy simulations (e.g., alternative stock structures and CPUE targets) with the same vector of parameters and random error terms. This allows us to compare independently the relative outcomes of each management strategy for each of the 1000 states of nature simulated.

Alternative stock management structures

We model three alternative stock management structures in addition to the current structure. For the current stock management structure, TACCs in both areas are adjusted with a decision rule (Appendix B) that uses CPUE from CRA8 only. However, separate TACCs are maintained and the CRA7 area maintains its size concession, allowing it to take smaller lobsters but also maintain its shorter season (5 months running from 21 June to 19 November for CRA7, compared with a 12-month season for CRA8 beginning in April). The season length for CRA7 is an important assumption in the model. Historically, catch has often fallen well short of the TACC. We assume catch is limited by the minimum of the TACC or a catch consistent with an exploitation rate equal to the average over the period 1990–2000 (Bentley et al. 2003*b*). Essentially, this assumes that fishing effort is capped at the average level of prior years and that catchability is assumed to remain unchanged.

The first alternative stock management structure is joint management. This is very similar to the current management structure, except that the decision rules operate using a weighted average of CPUE from both CRA7 and CRA8, as opposed to only CRA8 CPUE. Since CRA7 CPUE is lower than CRA8, the target CPUE is also proportionately lower.

For separate stock management strategies, the TACC for CRA8 is adjusted in the same manner as that for current management using CPUE in CRA8. However, a constant exploitation rate (CER) is maintained for CRA7. Under a CER strategy, the TACC would be set each year based on a target exploitation rate. We use CPUE as an index of vulnerable biomass and seek to maintain the current exploitation rate based on that index. A scalar is derived based on the recent annual ratios between catch and CPUE:

$$\bar{S} = \frac{\sum_{t=1990}^{2000} C_t/\mathrm{CPUE}_t}{11} \quad (11)$$

The TACC in each year could then be set by using the scalar with the predicted CPUE:

$$\mathrm{TAC}_t = \mathrm{CPUE}_t \cdot \bar{S} \quad (12)$$

This procedure for setting TACC would maintain a CER consistent with that in the last 11 years without the need to estimate vulnerable biomass in each year. The scalar calculated is 229.3 (Bentley et al. 2003*b*).

Under the amalgamated stock management structure, a combined TACC is set for the CRA7 and CRA8 areas. The decision rules used to adjust the TACC are based on CPUE in CRA8 just as they are for the current stock management. The size concession in the CRA7 area is removed as is the seasonal constraint. The larger minimum size reduces the available lobster in the CRA7 areas considerably and reduces CPUE to unprofitable levels. Consequently, we assume that all catch shifts from the CRA7 to the CRA8 after amalgamation. In reality, it is possible that CPUE might remain high in parts of CRA7 and fishing might continue there after amalgamation. However, we cannot predict or model this since we do not have data on the spatial heterogeneity of the CRA7 stock.

Decision rules

All of the management strategies simulated use decision rules based on commercial CPUE to adjust the TACC over time. The decision rule used for the current management strategy was designed for rebuilding the stock and is not expected to perform well at maintaining the stock at a particular level once it has been rebuilt. An alternative maintenance decision rule (Appendix B) for the maintenance stage was chosen from among those tested by Breen et al. (2003). Of the rules examined in that study that were based on maintaining a target CPUE, the Bentley gradient rule generally performed the best over a suite of performance criteria, including average and minimum catch and catch and biomass stability. We use that rule as the decision rule for the alternative management strategies in the maintenance stage once the rebuilding target has been reached. The current decision rule is still used for the rebuilding phase for all management strategies and is used for the entire period of the simulations of current management.

Results

In addition to current management, we evaluate nine management strategies, including each combination of the three alternative stock management structures and three CPUE targets. We compare the performance of different management strategies using multiple indicators, including average catch,

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the relative variability of catch over time, size composition of catch, PVNR, and VTQ.

In addition to the average of the performance indicators, we consider the distribution of outcomes that occur over the 1000 replications, each of which represent a possible state of nature. We indicate the 5th, 25th, 75th, and 95th percentile outcomes. Since all randomization is held constant across management strategies for each of the 1000 replications, we can also compare the relative performance of the management strategies for each potential state of nature. For each scenario, we calculate the ratio of a particular performance indicator (e.g., average catch or PVNR) for each replication relative to that indicator for that replication for the current management strategy. By considering the full distribution of the ratio across the 1000 different states of nature, we can estimate the probability the scenario would be expected to produce higher or lower average catch than that under current management, given the full range of states of nature modelled with the 1000 replications.

Average catch, variation in TACCs, and catch composition

We first consider the average annual catches over the 20-year period projected by the model for the different strategies. There are relatively small differences between average annual catches across management strategies (Fig. 3*a*). The strategies shown result in average annual catch values that are 95%–100% of the 695-t average achieved with the current management strategy. However, for a given policy scenario, a wide range of average catch levels are possible depending on the state of nature (i.e., the random parameterization of the simulation for a particular policy scenario).

The results are similar when we consider the average catch relative to that which results with current management for each of the 1000 random permutations (Fig. 3*b*). For certain states of nature, all of these management strategies could result in a higher average catch than current management, but current management will, on average, provide a higher average catch than any of the strategies that use the alternative rule. Thus, the high variability in average catch across management strategies is caused not only by random variation in recruitment, growth, movement, etc., but in how the different management strategies respond to those different states of nature.

The variability of TACCs also differs across management strategies. The average number of TACC changes over the 20-year period was greater than for current management for all of the scenarios using the alternative rule (Fig. 4). The combined TACC for CRA7 and CRA8 changes nearly every year for the separate management scenario, since the CRA7 TACC is tied directly to abundance. For joint management and amalgamation, the TACC changes every other year on average, which is the maximum possible given that the decision rule cannot trigger a TACC change 2 years in a row. In contrast, the TACC changes an average of eight times for the current management strategy. The average frequency of TACC changes differs little for amalgamation versus joint management.

However, this is only one indicator of catch variability. When variability is measured in terms of the coefficient of variation of interannual catch, the relative rankings of the different management strategies are reversed. For the various management strategies that use the alternative decision rule, the average (over the 1000 replications) of the coefficient of variation (CV) of annual catch across years is 5%–20% lower than that under current management. The CPUE target has little effect on the CV of interannual catch, but stock management structure has some effect. Separate management provides the lowest interannual variability of combined CRA7 and CRA8 catch. The CV of interannual catch for separate management is somewhat lower than for amalgamation, which in turn is lower than the CV for joint management. As with the other performance statistics, interannual variability of catch varies greatly across the 1000 replications for all management strategies.

We also tracked the percentage of replications for which the combined CRA7 and CRA8 TACCs fell below 50% of the current combined TACC at some point during the 20-year period modelled. This is an unlikely occurrence with any of the management strategies modelled, occurring in fewer than 6% of the replications for all management strategies. In general, the likelihood of occurrence is slightly greater for more conservative strategies with higher CPUE targets. For a given CPUE target, the frequency of the TACC falling below the benchmark is slightly higher for joint management than for amalgamation and is lowest for separate management. For example, for the current CPUE target, the TACC falls below the benchmark in 4.6% of the replications with joint management, 3.7% with amalgamation, 2.7% with management, and 0.8% with separate management. The lower rate of occurrence for separate management is due to the ability of the fishery to maintain a high exploitation rate on the smaller lobsters in the CRA7 area even when the biomass of legal size lobster in CRA8 is low.

The stock management structure affects the grade composition of catch (Fig. 5), as well as the total catch. Separate management increases the proportion of the catch made up by the smallest grades mainly as a result of increased total catch coming from CRA7. The opposite is true for amalgamation, which eliminates catch in the smallest grade and increases catch in the medium grades relative to current management. Joint management also shifts catch composition to larger sizes compared with current management, though less so than amalgamation. The CPUE target has only a very minor effect on grade composition of catch.

Profitability

The PVNR over the 20-year period modelled is a primary performance indicator that provides a direct means to quantify trade-offs between higher catches and revenues and lower harvest costs. We present both absolute results and results in terms of the ratios of PVNR relative to the current management strategy. The CPUE target has a very minor effect on the PVNR for the combined CRA7 and CRA8 areas (Fig. 6*a*). While average catches are, in general, higher for strategies with lower CPUE targets, the positive effect of higher catches is offset by higher harvest costs resulting from lower average CPUE. There are relatively small differences in the PVNR across stock structures. Amalgamation yields a slightly higher PVNR on average than joint management, which in turn yields a higher PVNR than separate management. As was the case for average catch, there is

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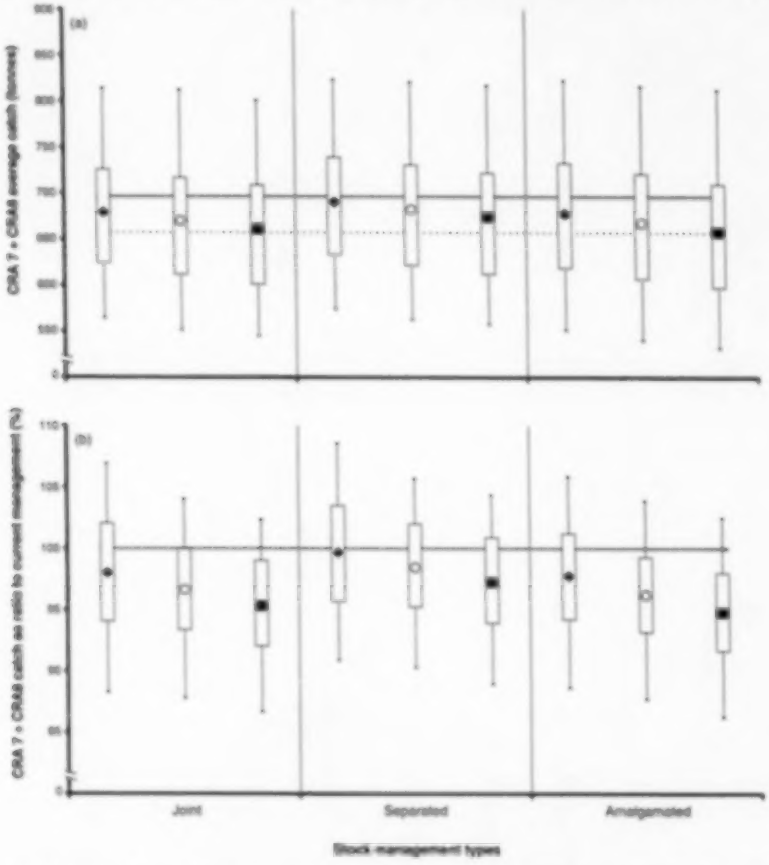
Fig. 3. (*a*) Average annual catch for the combined CRA7 and CRA8 fisheries between 2003 and 2022 and (*b*) the average ratio of the average combined CRA7 and CRA8 catch to that for the current management. The symbols indicate, for each stock strategy, the average of the performance indicator for CPUE targets 10% below (diamonds), equal to (circles), or 10% above the current CPUE target (squares). The box-and-whiskers plots show the 25th and 75th percentile (box) and the 5th and 95th percentile (whiskers) of the performance indicator from the 1000 replications. The horizontal lines in *a* and *b* show the average annual catch and the 100% ratio mark, respectively, for the current management strategy. The dotted horizontal line in *a* shows the 2001–2002 combined CRA7 and CRA8 TACC.



considerable variation in the PVNR across replications for a given policy scenario.

The ratios of outcomes taken on a replication-by-replication basis suggest somewhat greater differences between management strategies (Fig. 6*b*). With the current CPUE target or the target that is 10% lower than current CPUE, both joint management and amalgamation yield higher PVNRs than that achieved by current management for more than 75% of the replications.

Sensitivity to economic assumptions

Prices on average have historically been considerably higher in the AW season than in the SS season, and consequently, catches are concentrated in the AW season. The prices and seasonal catch distribution we use in the modelling reflect this. However, increased stock sizes and higher CPUE could allow an even greater concentration of catch in the AW season. We consider the effects on the performance of the different management strategies of a 20% shift of catch from the SS season to the AW season. Even though CPUE is lower and per unit harvest costs are higher in the AW season, price effects tend to dominate the effect of increasing harvest costs. The shift of catch to the AW season would increase profitability for all management strategies relative to current management (Fig. 7). However, the relative rankings of the different management strategies are unaffected.

The base model assumes different prices by grade and season. The prices used are derived by calculating seasonal averages from monthly average prices in the 2001–2002 season. Prices were generally higher for medium and large lobsters than for the small or very large lobsters (Table 1) and were also generally higher in CRA8 than in CRA7. Prices were also higher in the AW season than in the SS season. It is quite possible that the price advantages of particular grades or times of year could change over time. Several years ago, the smallest grades taken in the CRA7 area received a price premium. The AW seasonal price advantages results from an absence of production from large Australian fisheries at that time of year due to seasonal closures, but increasing production from other countries like South Africa or changes in Australian seasonal closures could reduce that price pre-

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Fig. 4. Average number of TACC changes over the 20-year simulation period. The symbols indicate, for each stock strategy, the average of the performance indicator for CPUE targets 10% below (diamonds), equal to (circles), or 10% above the current CPUE target (squares). The box-and-whiskers plots show the 25th and 75th percentile (box) and the 5th and 95th percentile (whiskers) of the performance indicator from the 1000 replications. The horizontal line shows the average number of TACC changes for the current management strategy.

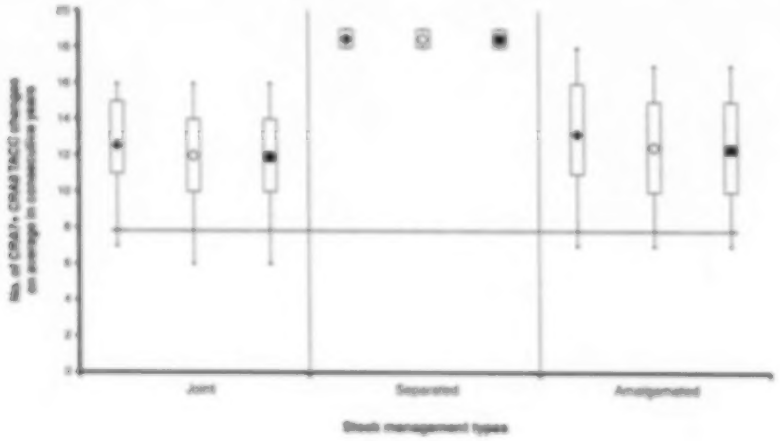
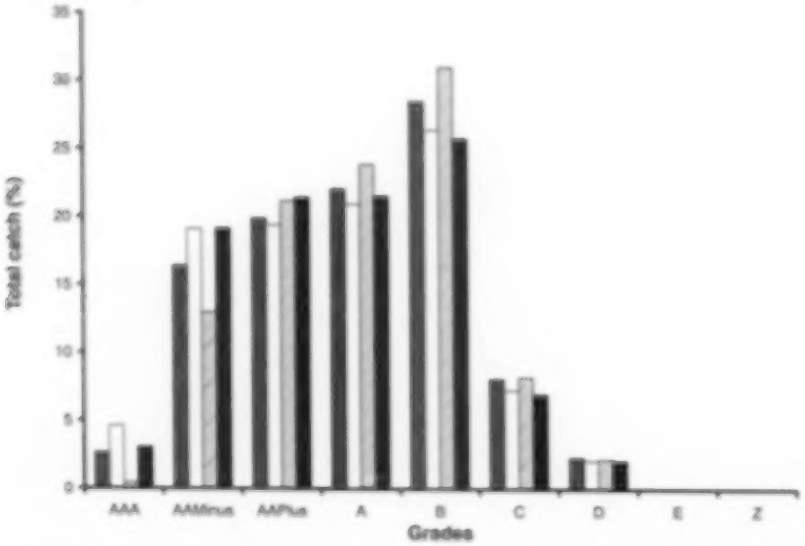


Fig. 5. Proportion of total catch by grade for the current CPUE target under different stock management structures. The columns show the average proportion of total catch in that grade for simulations of joint management (shaded), separate management (open), amalgamation (hatched), and current management (solid).



mium. To isolate the effect that the differences in prices across grades and seasons are having, we present results from a model that applies the same price for all lobster regardless of grade or season. We use an average price equal to the overall average price that results from the current management scenario (e.g., the average of total revenues divided by total catch). The price assumptions do have some impact on the performance of amalgamation relative to other stock structures (Fig. 8). For joint management, the price assumptions have little impact on relative outcomes. However, the relative advantage of amalgamation is almost eliminated when the price differential is removed. The opposite is true for separate management for which PVNR increases somewhat under this assumption about prices.

We also considered the impact of a general reduction in prices. When prices for all grades, seasons and areas were reduced by 20%, the relative ranking of the management strategies, in terms of PVNR, was unchanged. However, the percent difference in average PVNRs among strategies and relative to current management was increased. Decreased prices shrink profit margins and increase the relative benefits from strategies that maintain higher profit margins.

The use of a present value criterion to rank strategies allows us to compare strategies with different temporal paths

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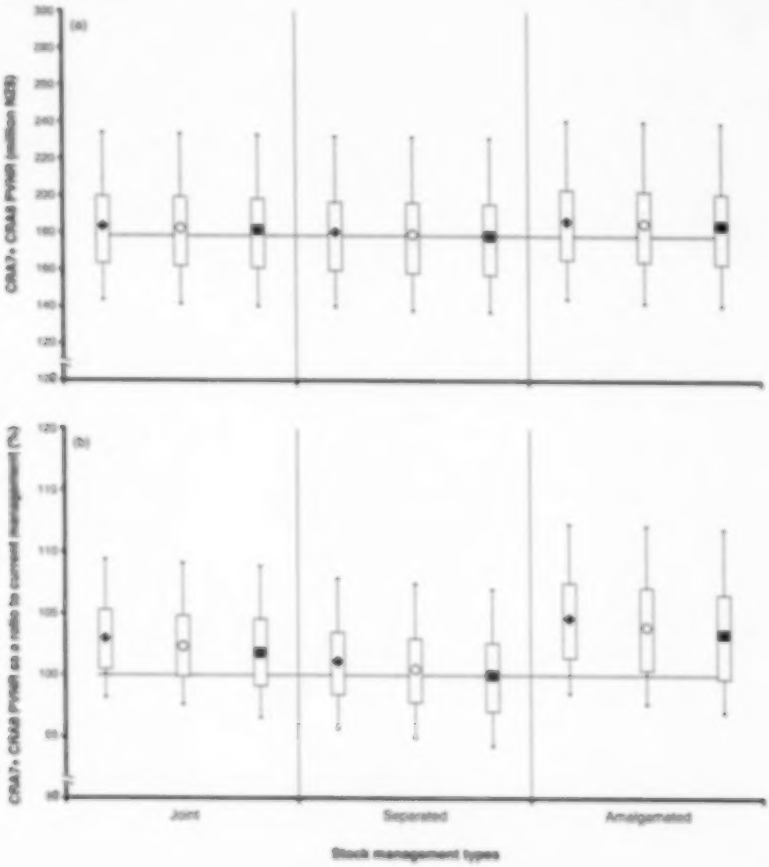
Fig. 6. (*a*) PVNR for the combined CRA7 and CRA8 fisheries between 2003 and 2022 and (*b*) the ratio of PVNR from the combined CRA7 and CRA8 catch relative to that for current management. The symbols indicate, for each stock strategy, the average of the performance indicator for CPUE targets 10% below (diamonds), equal to (circles), or 10% above the current CPUE target (squares). The box-and-whiskers plots show the 25th and 75th percentile (box) and the 5th and 95th percentile (whiskers) of the performance indicator from the 1000 replications. The horizontal lines in *a* and *b* show the average PVNR and the 100% ratio mark, respectively, for the current management strategy.



of benefits. Since the pay-off for more conservative management approaches may take a very long time, this can be very important. It does, however, bring up the issue of the appropriate discount rate to use. We present results using an 8% discount rate because that roughly reflects the real discount rate in New Zealand for commercial investments of similar risk. This may be appropriate from the point of view of commercial stakeholders, but noncommercial stakeholders might evaluate temporal trade-offs using a lower discount rate. Some stakeholders may also use higher discount rates to evaluate financial decisions. We examined the sensitivity of results to the discount rate by applying a range of discount rates from 0% to 18%. Changes in the discount rate do not affect the relative rankings, in terms of their PVNR, of the nine principal management alternatives. In general, the higher the discount rate, the smaller the difference between the different alternatives. For example, with a zero discount rate, the average PVNR for amalgamation with current CPUE target and the alternative rule is 8% higher than that under current management, while the average PVNR is only 4% higher with an 8% discount rate and only 2% higher when an 18% discount rate is applied. The reason for this result is that the strategies with higher profitability tend to defer gains longer, and higher discount rates reduce the present value of those future gains.

Distributional impacts

The relative effects on catch and average PVNR of different management strategies are quite different for quota owners in the CRA7 and CRA8 areas. The CPUE target has relatively little effect on the benefits that are expected to accrue to quota owners from the two QMAs, but the stock structure has significant and contrary impacts for the two groups. Under the amalgamation strategies, there is, by assumption, no longer any catch taken from the old CRA7 QMA. However, the CRA7 quota is used in what was the old CRA8 QMA.

The VTQ for CRA7 is considerably increased under amalgamation relative to current, joint, or separate management (Fig. 9*a*). This is expected since the current price of a tonne

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Fig. 7. PVNR for the combined CRA7 and CRA8 fisheries between 2003 and 2022 with 20% seasonal shift of catch to AW. The symbols indicate, for each stock strategy, the average of the performance indicator for CPUE targets 10% below (diamonds), equal to (circles), or 10% above the current CPUE target (squares). The box-and-whiskers plots show the 25th and 75th percentile (box) and the 5th and 95th percentile (whiskers) of the performance indicator from the 1000 replications. The horizontal line shows the average PVNR for the current management strategy.

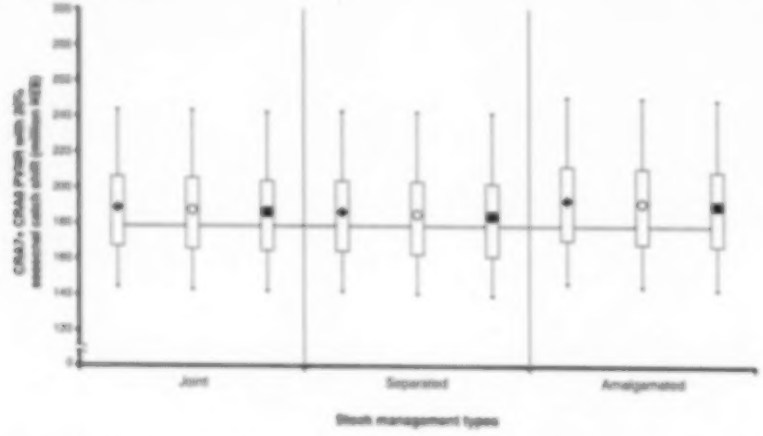
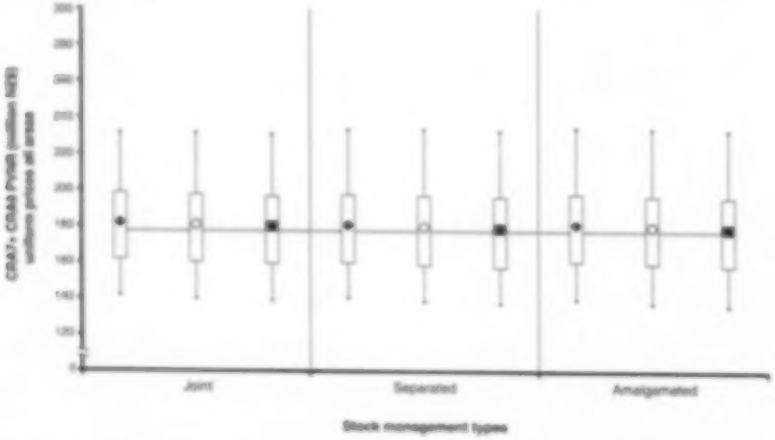


Fig. 8. PVNR for the combined CRA7 and CRA8 fisheries between 2003 and 2022 with equal prices for all grades and seasons. The symbols indicate, for each stock strategy, the average of the performance indicator for CPUE targets 10% below (diamonds), equal to (circles), or 10% above the current CPUE target (squares). The box-and-whiskers plots show the 25th and 75th percentile (box) and the 5th and 95th percentile (whiskers) of the performance indicator from the 1000 replications. The horizontal line shows the average PVNR for the current management strategy.



of CRA8 quota is considerably higher than a tonne of CRA7 quota as a result of higher average prices and profit margins in CRA8. CPUE is also higher in CRA8, but higher costs per unit of nominal effort tend to offset the benefits of higher catch rates somewhat. Separate management also increases the VTQ for CRA7, though less than amalgamation. However, when the model is run assuming the same price for all grades and areas, the highest VTQ for CRA7 is achieved under separate management followed by amalgamation.

The results are quite different from the perspective of CRA8 quota owners (Fig. 9*b*). While amalgamation results in slightly higher VTQ for CRA8 than under separate management, it results in a lower VTQ on average than under joint management. Both amalgamation and joint management on average yield higher VTQ for CRA8 than under current management.

Discussion

These simulations are not meant to identify an optimal management alternative, but rather to provide stakeholders with the information they need to choose among alternatives. Management strategy evaluation using fishery simulation modelling offers a means to identify management strategies that are cost effective, robust to uncertainty, and consistent with the objectives of stakeholders and managers. Adding an economic component that objectively quantifies trade-offs between higher revenues and lower costs, as well as differences in the temporal stream of benefits, can enhance the

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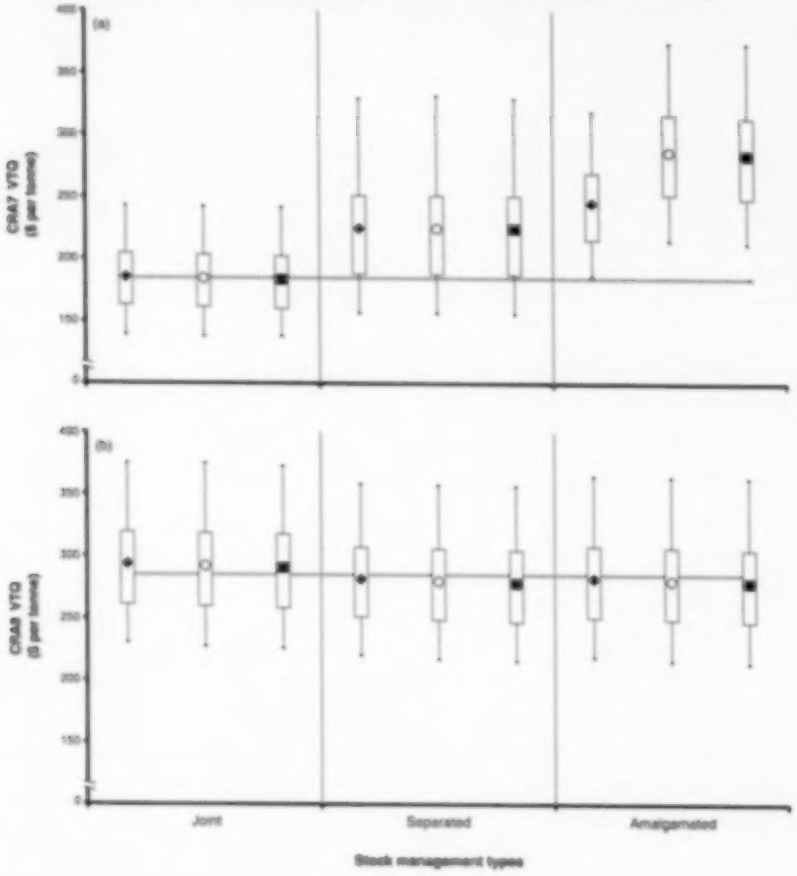
Fig. 9. VTQ (NZ$ per tonne) for *(a)* CRA7 and *(b)* CRA8. The symbols indicate, for each stock strategy, the average of the performance indicator for CPUE targets 10% below (diamonds), equal to (circles), or 10% above the current CPUE target (squares). The box-and-whiskers plots show the 25th and 75th percentile (box) and the 5th and 95th percentile (whiskers) of VTQ from the 1000 replications. The horizontal lines in *a* and *b* show the average VTQ under the current management strategy.



ability of managers and stakeholders to make sound decisions. However, stakeholders may have diverse and conflicting objectives, and a mean prediction of profitability is only one of multiple indicators relevant to evaluating the performance of alternative strategies.

The simulations showed relatively small differences in performance (both biological and economic) across management strategies. Additionally, the wide range of outcomes over the 1000 replications precludes any definitive performance ranking of the different strategies. As the figures showing the ratio of indicators for each state of nature demonstrate, variation in the relative performance, as well as the absolute performance of the management strategies, is a function of uncertain variables and stochastic processes. If uncertainty in model parameters and processes can be reduced, it may be possible to identify superior management strategies more clearly. However, much of that uncertainty is inherently unpredictable and is unlikely to be resolved. This is particularly true of recruitment, which is a primary driver of variability in outcomes across replications. Assumptions about migration are also critical, particularly when considering amalgamation. More tagging studies are needed to reduce the uncertainty associated with this process.

While differences in performance are small, it is notable that the economic performance indicators (i.e., PVNR) provide rankings of management strategies that are contrary to those based on average catch levels. This is a result of differences in the size composition of catch and prices across areas, and of the effects of lower costs that are achieved by maintaining higher CPUE. In the case of amalgamation, catch is shifted from the CRA7 area, which had smaller margins between revenue and cost per kilogram of lobster to the CRA8 area, where margins are higher. The relative difference between the biological and economic indicators would be even greater if the average prices of the lobsters decreased, which has, in fact, occurred since the price data was assembled. Lower prices squeeze profit margins and increase the importance of maintaining lower harvest costs.

This analysis highlights the importance of considering distributional effects. Differences in overall catch and profitability across management strategies are not large and are subject to a good deal of uncertainty. Consequently, distribu-

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tional issues may well prove more important than overall net benefits in the decision making process. While the simulations suggest that the net value of the combined CRA7 and CRA8 fishery would be increased by amalgamating the two areas, it also appears that the gains from this policy would accrue to CRA7 quota owners, while CRA8 quota owners may in fact be slightly worse off than they would be with joint management. When presented with these results, quota owners in CRA8 who are also fishers expressed concern that the shift of quota might lead to more fishing in the area they fish, which could decrease their catch rates. Although this appears unlikely given that overall effort is predicted to decline, the model was not able to address this question directly. There may also be important negative effects on non-quota owners as a result of shifting catch from CRA7 to CRA8. Part-time lobster fishers in CRA7 who relied on leasing quota would probably no longer be able to continue fishing lobster. They may lose a significant portion of their income, which they may find difficult to replace.

The New Zealand government is encouraging increased involvement of fishery stakeholders in management of their fisheries by empowering them to develop fishery plans that can include management procedures for determining TACCs, among other things. This has increased the interest of commercial stakeholders in developing the means to predict the likely economic and biological results of alternative management strategies, which requires not only new models but also new data collection activities. This work was done at the request and expense of the seafood industry. The economic data used for this model are not collected by the government, and this type of bioeconomic analysis has not traditionally been part of management decision making for New Zealand fisheries. However, we expect that increased use of fishery plans will provide sufficient incentives for commercial stakeholders to provide the funding and confidential economic data necessary to undertake this type of analysis.

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Appendix A. Biological model description

The structure and parameterization of the biological model is based on the 2000 NSS stock assessment (Bentley et al. 2001) and addresses the uncertainty associated with the assessment by sampling sets of parameters from the joint posterior distribution of the fully Bayesian assessment and allowing for stochastic variation in other uncertain parameters and processes. A more comprehensive description of the stock assessment including details on the joint posterior distributions of parameters has been published elsewhere (Bentley et al. 2001). In each of the runs, stochastic process and observation error were simulated, and a random state-of-nature was obtained with respect to the stock–recruit dynamics and migration with specified ranges or distributions of process error, observation error, state-of-nature distributions and projection errors (Table A1).

Migration

The model operates on a semiannual time step with an AW season followed by a SS season. A unidirectional migration pattern is modelled with lobster moving from Otago to Steward Island or Fiordland and from Stewart Island to Fiordland. Migration occurs at the start of the SS season. Lobsters are thought to migrate from Otago into Southland just before the onset of maturity (Booth 1997). We modelled the probability of individual lobsters moving H, as a logistic function, with the size at 50% probability of the migrating

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Table A1. Parameter distributions used in simulations.

Parameter	Distribution
Egg production *a*	*F*(0.06)
Egg production *b*	*F*(3.18)
Standard deviation of larval survival	*U*(0.5,1)
Density dependence in settlement *Z*	*U*(0.75,0.95)
Growth parameters G50 and G80 for each sex	Po
Growth Coefficient of Variation	*F*(0.373)
Growth Std. Deviation and Minimum	*F*(1)
Natural mortality rate M	Po
Migration:	
Difference between size at 50% maturity and size with 50% probability of migrating	*U*(–15,–5)
Observation error for CPUE	*L*(1,0.2)

Note: *F*(*x*), fixed at *x*; *U*(*a*,*b*), uniform distribution from *a* to *b*; Po, sampled from the posterior distribution; *L*(*a*,*s*), lognormal distribution with mean *a* and standard deviation *s*.

set to be d mm tail width (TW) less than the size at which the probability of maturing is 50% m_{50}

$$H_s = \frac{1}{1+\exp\left[\frac{-\ln(19)(\bar{S}_s - m_{50} - d)}{w}\right]} \quad \text{(A1)}$$

where $\bar{S}_s$ is the mean size of animals in the sth size class. The steepness of this function is determined by w, and we assume this to be the same as the steepness of the maturation curve. The size of maturity for males is unknown and was assumed to be the same size as for females. The number of lobsters eligible to migrate is determined from the size distribution and migration ogive described above. The proportions migrating, as well as their destinations, are determined by three parameters: A, B, and C (Table A2).

Table A2. Matrix of migration.

	Destination		
Source	Otago	Stewart Is.	Fiordland
Otago	1-*A*-*B*	*A*	*B*
Stewart Is.	0	1-*C*	*C*
Fiordland	0	0	1

Note: The rows and columns represent sources of migrants and destination of migrants, respectively. Values or expressions in the cells represent the proportion of migrants from that source that migrate to that destination. *A*, *B*, and *C* are uniformly distributed random numbers, with *A* and *B* ranging from 0.15 to 0.45, and *C* distributed between 0.10 and 0.80.

Table A3. Matrix of the dispersion of larvae in the first scheme.

	Destination		
Source	Otago	Stewart Is.	Fiordland
Otago	1.0	0.0	0.0
Stewart Is.	0.5	0.5	0.0
Fiordland	0.3	0.3	0.4

Note: The rows and columns represent sources of larvae (eggs) and the destination of larvae, respectively.

Stock–recruitment

Total egg production in each area during each time period ($E_{t,a}$) was modelled using an exponential fecundity-at-size relation and numbers of mature females

$$E_{t,a} = \sum_s N_{t,a,s}^{\text{femmat}} \phi \bar{S}_s^b \quad \text{(A2)}$$

where $N_{t,a,s}^{\text{femmat}}$ is the number of mature females at time t, in area a, in size class s, and $\bar{S}_s$ is the mean size of animals in the sth size class. The same values for the parameters ϕ and b were used for all three areas.

For each run in the sets of evaluations, the model randomly chose, with equal frequency, between two alternative egg-dispersal schemes. In the first scheme, larval production from each area is made proportional to egg production in each area, and larvae are distributed among areas (Table A3). Because of the predominately westward flow of currents in the area, we assume that all Otago eggs produce Otago larvae, and that Fiordland eggs produce larvae in all three areas. In the second scheme, the model assumes that the source of larvae is external to the stock and, thus, the number of larvae is unrelated to local egg production. In this scenario, total larval supply has a mean equal to that for the unfished stock and is distributed 20% to Otago, 30% to Stewart Island, and 50% to Fiordland.

A density-dependent stock–recruit function was applied before larvae recruit to the model. Throughout this paper, recruitment refers to recruitment to the first size class in the model rather than to settlement of larvae or recruitment to the fishery. Density-dependent postsettlement survival was modelled using a Beverton–Holt stock–recruitment relationship parameterized using virgin recruitment R_0 and steepness z. Stochastic variation in settlement was simulated by applying a stochastic multiplier R_t to the total numbers of larvae transported to each area. A multiplier of one implies the mean rate of larval survival. Multipliers were generated independently for each of the three areas from a lognormal distribution with a mean of 1 and a standard deviation of σ^s

$$N_{t,0}^S = \frac{S_t}{\alpha + \beta S_t} R_t \quad \text{(A3)}$$

$$\alpha = S_0 \frac{1-z}{4zR_0} \quad \text{(A4)}$$

$$\beta = \frac{5z-1}{4zR_0} \quad \text{(A5)}$$

where S_0 is the mean egg production from the virgin stock.

Growth, mortality, and catch

The model simulates the numbers of lobsters in each of thirty-one 2-mm tail-width (TW) size classes for each sex. Females are separated into immature and mature categories so that the effect of the prohibition on the taking of oversized females on exploitation rates and vulnerable biomasses can be replicated. Natural mortality and fishing mortality occur at each time step. Natural mortality is assumed to be constant and independent of size. Fishing mortality is ap-

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plied using a size selectivity curve and different vulnerabilities for each sex during each season.

Moult-based growth is modelled by specifying the sex- and size-specific moult increment of a lobster in a specific size class and sex, size and season specific probability of moulting. Together, these specifications determine the growth of population components to large size classes.

The simulation model allows the proportion of the annual TACC that is taken in each season (AW and SS) to be changed from a starting seasonal split. The initial split was calculated separately for CRA7 and CRA8 based on the average of the split over the years 1999–2000 to 2001–2002. The base model assumes 71% of the CRA7 catch and 54% of the CRA8 catch is taken in theAW season. The model calculates the breakdown of catches for each of nine commercial weight grades (Table 1) based on the relative abundance of lobster of each grade. The model requires specification of the proportion of the CRA8 TACC taken in the Stewart Island (statistical areas 922, 923, 924, 925) and Fiordland (926, 927, 928) areas. This is fixed at the average of the proportion of the catch taken in over the years 1999–2000 to 2001–2002.

Vulnerable biomass and CPUE

Although the model has a semiannual time step, the CPUE used in operating the decision rule is an annual CPUE, so the relative vulnerabilities for each sex category during each season are combined using the proportion of catch taken during each season in CRA8. All mature females are assumed to be ovigerous in the AW season and are not considered part of the vulnerable biomass. The CRA7 MLS is a 127-mm tail length (TL) for both sexes; the CRA8 MLS for males is a 54-mm TW and a 57-mm TW for females. For CRA7, the length at maximum selectivity was assumed to be the CRA7 MLS. The MLS limit in CRA7 is a 127-mm TL. Since size regulation in CRA7 is by TW, we converted this to TW using coefficients for a linear relationship between TL and TW for CRA7.

Starting conditions

Because the operating model incorporates stock-recruitment relations, it is inappropriate to use the estimate of average recruitment from the 2000 NSS assessment, which did not assume a stock–recruitment relation. Rather, we assume that the population in 2000 is in equilibrium with the exploitation rate, $\overline{U}$, estimated from the most recent NSS assessment (Bentley et al. 2001). Those authors estimated a range of 41%–59% exploitation rate.

The starting population is initialized, given the particular movement and settlement dynamics, and the exploitation rate and an arbitrary fixed virgin recruitment. It is assumed that virgin recruitment is distributed as 20% to Otago, 30% to Stewart Island, and 50% to Fiordland.

When the population reaches equilibrium with the exploitation rate, a catchability coefficient q was calculated as a simple ratio between the equilibrium vulnerable biomass B_{eq} and the observed CPUE in 1999 (Table A4):

$$q = \frac{\text{CPUE}_{1999}}{B_{eq}} \quad \text{(A6)}$$

Table A4. Mean CPUE and annual commercial catch in each area in 1999 from Bentley et al. (unpublished data).

Area	Standardised CPUE (kg·pot lift^{-1})	Catch (t)
Otago	0.32	56.5
Stewart Island	1.00	94.0
Fiordland	1.00	615.8
CRA7 + CRA8	0.75	756.3

Similarly, Q, a scalar between the equilibrium catch (the product of the vulnerable biomass and the exploitation rate) and observed catches in 1999 (Table A4), was calculated as follows:

$$Q = \frac{C_{1999}}{B_{eq}\overline{U}} \quad \text{(A7)}$$

The calculated Q and q were used to scale the simulated catch and CPUE, respectively.

Appendix B. Decision rules

The simulations use one of two decision rules to adjust the TACCs over time. The rule used for current management was specifically designed for rebuilding the stock over a fixed timeline. To model alternative management strategies, we impose an alternative rule once the target has been met.

Current rule

The rule used for current management calculates a multiplier Z that is used to determine the new total allowable catch TAC_{yr2} from the existing catch TAC_{yr1}:

$$\text{TAC}_{yr2} = Z_y\text{TAC}_{yr1} \quad \text{(B1)}$$

The Z_y is calculated from observed and target values for CPUE and from three parameters of the rule: N, the number of years used for averaging CPUE in the rule; W, relative weight given to the distance between observed and target CPUE, relative to the difference between target and observed gradients; and S, a scaling or sensitivity parameter used to determine the rule's response. These three parameters (Table B1) thus define a large family of candidate decision rules.

The difference between target CPUE (I_t^{tar}) and observed CPUE (I_t^{obs}) is calculated in a status indicator for each year of data.

$$A_t^0 = I_t^{obs}/I_t^{tar} - 1 \quad \text{(B2)}$$

During the rebuilding stage, the predicted CPUE is the taken from the linear rebuilding trajectory shown in Fig. 2. Once the rebuilding target has been reached, the target CPUE remains at the rebuilding target.

The difference between the target and observed gradient is calculated in a gradient indicator:

$$A_t^g = ((I_t^{obs} - I_{t-1}^{obs})/I_{t-1}^{obs}) - ((I_t^{tar} - I_{t-1}^{tar})/I_{t-1}^{tar}) \quad \text{(B3)}$$

Each is averaged for N years:

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Table B1. Parameters of the current NSS harvest control rule and the alternative rule.

Parameter	Value
Current NSS decision rule	
N, number of years in running average for both the status and gradient indicators	3
W, relative weight for the status indicator	0.40
S, scalar for management decision	0.75
Minimum, minimum management action accepted	0.05
Maximum, maximum management action accepted	0.25
Alternative rule	
s, scalar adjusting the severity with which rule is applied	0.02
T_{min}, minimum percent change made to TACC	0.05
T_{max}, maximum percent change made to TACC	0.25

(B4) $$\bar{A}_t^{\circ} = \frac{1}{N} \sum_{d=t-N+1}^{d=t} A_d^{\circ}$$

and similarly for A_t^{β} to obtain $\bar{A}_t^{\beta}$. The mean gradient A_t° and status indicators are combined, using the relative weight W:

(B5) $$A_t^{*} = W\bar{A}_t^{\circ} + (1 - W)\bar{A}_t^{\beta}$$

Now the combined mean indicator is used with the scalar S to determine a response R_t:

(B6) $$R_t = SA_t^{*}$$

This response is then used to determine the multiplier Z_t, taking into account the sign of R_t, and limiting the magnitude with minimum and maximum thresholds. The minimum threshold is 0.05, and the maximum is 0.25.

(B7) $$Z_t = 1 \quad \text{for } -0.05 \le (R_t) \le 0.05$$

$$Z_t = 1 + R_t \quad \text{for } -0.25 \le (R_t) < -0.05 \text{ and for } 0.05 < (R_t) \le 0.25$$

$$Z_t = 0.75 \quad \text{for } (R_t) < -0.25$$

$$Z_t = 1.25 \quad \text{for } (R_t) > 0.25$$

A latent year is specified, prohibiting changes to TACC in two consecutive years.

Alternative rule

The rule used for the alternative management strategies, once the rebuilding target has been met, adjusts TACC based on a ratio between the CPUE index and the value of the index the last time that the quota was changed. In this way, the rule is similar to a constant exploitation rate rule in that it tries to keep catches proportional to vulnerable biomass. In addition, to maintain the target, the rule changes the response according to the distance of CPUE from the target.

The rule has a target CPUE I^{*}, and its parameters are a sensitivity parameter s and threshold levels for the minimum change T_{min} and the maximum change T_{max}. The rule calculates two intermediate values: the response R and the distance D.

(B8) $$R_t = \bar{I}_t / \bar{I}_{t-x}$$

where x is 1 if the TACC changed in year $t - 1$ and 2 if the TACC was changed in the year before that, and so on.

(B9) $$D_t = 1 + (\bar{I}_t / I_t^{*} - 1)s$$

The amount by which the TACC changes Z_t is then modified by the thresholds:

(B10) $$Z_t = \begin{cases} 1 & |1 - R_t D_t| < T_{min} \\ R_t D_t & |1 - R_t D_t| \ge T_{min} \text{ and } |1 - R_t D_t| < T_{max} \\ T_{max} & |1 - R_t D_t| \ge T_{max} \end{cases}$$

(B11) $$\mathrm{TAC}_{t+2} = Z_t \mathrm{TAC}_{t+1}$$

Higher values of s mean that the rule tries harder to maintain the target but causes greater fluctuations in TACC and CPUE. Breen et al. (2003) used $s = 0.01$. After trials, we used a slightly higher value of 0.02 to maintain CPUE closer to the target. We used $T_{min} = 0.05$ and $T_{max} = 0.25$.

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A method to bin alleles of genetic loci that maintains population heterogeneity

Jeffrey F. Bromaghin and Penelope A. Crane

Abstract: Fishery resources are often studied when individuals from multiple stocks are aggregated. For that reason, mixed-stock analysis (MSA), i.e., estimation of the stock composition of a mixture of individuals, is an important component of many research programs. Although many characteristics can be used in MSA, DNA loci, particularly microsatellites, have become extremely common. Microsatellite loci usually have a greater number of potential expressions, or alleles, than other marker types. A high degree of polymorphism can enhance the power of MSA, but allele proportions are estimated less precisely and rare alleles are absent or observed in very small numbers in typically sized samples. The reduced precision and presence of rare alleles can degrade the performance of some analytic methods. Although the effect can be reduced by binning alleles, which is common, an objective method of doing so has not been available previously. We present a method for binning alleles that reduces the number of rare alleles, largely preserves the genetic relationships observed among stocks, and modestly improves the performance of mixed-stock and individual-assignment analyses. The method is illustrated with data from Yukon River chum salmon (*Oncorhynchus keta*) and western Alaska Dolly Varden (*Salvelinus malma*).

Résumé : On étudie souvent les ressources halieutiques dans des conditions où des individus de plusieurs stocks sont rassemblés. C'est pourquoi, l'analyse des stocks mixtes (MSA), c'est-à-dire l'estimation de la composition des stocks composés d'un mélange d'individus, fait partie intégrale de nombreux programmes de recherche. Bien qu'on puisse utiliser plusieurs caractéristiques dans les MSA, on emploie très couramment les locus ADN, particulièrement les microsatellites. Les locus microsatellites possèdent généralement un nombre plus élevé d'expressions potentielles, ou d'allèles, que les autres types de marqueurs. Un haut degré de polymorphisme peut améliorer la puissance des analyses MSA, mais les proportions des allèles ne peuvent être mesurées avec autant de précision et les allèles rares sont absents ou observés en très petits nombres dans les échantillons de taille ordinaire. La réduction de la précision et la présence des allèles rares peuvent diminuer la performance de certaines méthodes analytiques. Bien que l'effet peut être réduit par la mise en lots des allèles, ce qui arrive souvent, il n'y avait pas jusqu'ici de méthode objective pour le faire. Nous présentons une méthode de mise en lots des allèles qui réduit le nombre d'allèles rares, qui conserve en grande partie les relations génétiques observées entre les stocks et qui améliore marginalement la performance des analyses de stocks mixtes et d'assignations d'individus. Nous fournissons des exemples de la méthode à l'aide de données sur le saumon kéta (*Oncorhynchus keta*) du fleuve Yukon et la Dolly Varden (*Salvelinus malma*) de l'ouest de l'Alaska.

[Traduit par la Rédaction]

Introduction

Mixed-stock analysis (MSA) employing genetic markers is a common and useful tool in the study and management of fishery resources (e.g., Hallerman 2003). Originally applied to identify harvest components in mixed-stock fisheries (e.g., Grant et al. 1980), MSA is an increasingly vital method in harvest management and fishery research. Historically, MSA studies have tended to rely on data from allozyme loci. However, the number of DNA loci available for use in genetic studies has increased rapidly, especially microsatellite loci, and use of DNA loci is now routine.

The increased polymorphism of microsatellite loci inherently increases the power of genetic techniques in some applications (Ward and Grewe 1994). However, use of the full range of dimensionality, i.e., numbers of loci and alleles, in a data set is not necessarily advantageous. Smouse et al. (1994) and Smouse and Chevillon (1998) recommend use of a moderate number of both loci and alleles in MSA. Bernatchez and Duchesne (2000) demonstrate that there is a positive, but asymptotic, relationship between the number of alleles at a locus and the probability of correct population assignment. Selecting a subset of the loci available for MSA by criteria such as gene diversity, heterozygosity, or F_{ST}

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J.F. Bromaghin.[1] US Fish and Wildlife Service, Division of Fisheries and Habitat Conservation, 1011 E. Tudor Road, Anchorage, AK 99503, USA.
P.A. Crane. US Fish and Wildlife Service, Conservation Genetics Laboratory, 1011 E. Tudor Road, Anchorage, AK 99503, USA.

[1]Corresponding author (e-mail: Jeffrey_Bromaghin@fws.gov).

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(Scribner et al. 1998) or through empirical testing (Banks et al. 2003) can result in estimates nearly as accurate and precise as those obtained with full data sets.

One problem with using highly polymorphic loci is that larger sample sizes are needed to precisely estimate the allele composition of a population (O'Connell and Wright 1997). Most researchers have not tended to increase sample sizes commensurate with the polymorphism of the loci being used, resulting in an overall reduction in the precision of allelic composition estimates. However, if alleles are numerous and especially if many are rare, increasing sample sizes is not a feasible approach to maintain precision. Reduced precision is particularly problematic when analytical methods assume the genetic composition of baseline, or learning, samples reflect population parameters without error, as in MSA using conditional maximum likelihood methods (Pella and Milner 1987).

A second, related, problem is that rare alleles may be absent from some, or perhaps even all, baseline samples. The most commonly used estimator of allele composition is the maximum likelihood estimator, i.e., the ratio of the number of alleles of each type observed in a sample to the total number of all alleles. Alleles that are not observed in some baseline samples are thereby assumed to be absent from those populations. Such, presumed, sampling zeros are extremely influential. The genotype of an individual in a mixture sample may match the profile of a particular population nearly perfectly, but if the individual possesses a single rare allele not observed in the baseline sample, the estimated probability of belonging to that population is zero. For this reason, sampling zeros can degrade the performance of conditional maximum likelihood estimation (Pella and Masuda 2001), as well as individual-assignment analyses using the maximum likelihood estimator of allele composition (Bernatchez and Duchesne 2000).

Several approaches may relax the assumption that baseline allele proportions are known without error, or alleviate its influence, in MSA. The first is to use a method other than conditional maximum likelihood to estimate mixture proportions. Unconditional maximum likelihood methods, which simultaneously estimate baseline allele composition and mixture composition, might be employed. However, a large number of parameters must be estimated and estimates of the allele composition of baseline populations are not fixed from analysis to analysis. Brown et al. (1999) did not find substantial differences between estimates obtained via conditional and unconditional maximum likelihood, although additional comparisons might be warranted. Estimators of mixture composition based on other techniques, such as individual assignment or least squares, may be more robust to violations of this assumption than likelihood methods, but explorations have been limited. Millar (1990) found that maximum likelihood estimation is generally preferable to classification-based estimators, though all estimators he considered were conditioned on the observed baseline data. Researchers have recently begun to experiment with Bayesian methods of MSA (e.g., Pella and Masuda 2001). The Bayesian approach specifies a probability distribution for samples of allele composition and thereby reduces the influence of observed zeros in baseline samples. While Bayesian methods appear promising, whether or not they will be widely adopted or are computationally feasible for studies involving a large number of populations remains unclear.

A second approach is to use methods other than maximum likelihood to estimate the allele composition of the baseline populations and conditional maximum likelihood estimation thereafter. Although numerous allele composition estimators are available (Johnson et al. 1997), Bayesian estimators based on the Dirichlet probability distribution have been commonly used in fishery applications (e.g., Rannala and Mountain 1997; Cornuet et al. 1999; Pella and Masuda 2001). Two Bayesian estimators have been added to version 3.7 of the widely used MSA computer program SPAM (Lisa Seeb, Alaska Department of Fish and Game, Commercial Fisheries Division, 333 Raspberry Road, Anchorage, AK 99518, USA, personal communication). One property of these estimators is that estimates are numerically similar to maximum likelihood estimates and might therefore be assumed to partially share the theoretical properties of maximum likelihood estimators (Rao 1973). A second property is that all estimates are nonzero. If one assumes that alleles not observed in some or even all baseline samples are actually present in all populations, these estimators are probably preferable to the maximum likelihood estimator in many applications. While use of an alternative estimator does not eliminate the assumption that baseline allele proportions are known perfectly, it may reduce the potentially negative impact of presumed sampling zeros in both mixed stock and individual assignment analyses. For example, Kalinowski (2004) used computer simulation to conclude that small samples are adequate in MSA studies using highly polymorphic loci when a Bayesian estimator of allele composition is used, although the applicability of his findings in studies of natural populations remains uncertain.

A third approach is to bin alleles. While this does not eliminate the assumption that baseline allele proportions are known without error, it does reduce the influence of sampling error and potentially reduces the number and therefore influence of rare alleles. Researchers commonly bin alleles based on allele size and frequency criteria (Small et al. 1998; Beacham et al. 2001; Buonaccorsi et al. 2001). Although binning rare alleles has obvious practical advantages, there is limited theoretical support for either binning strategy. One drawback to both methods is that no measure of population differentiation is incorporated. Both methods may result in unnecessary loss of information, which is fundamental to many analytical methods, and the number of bins created and their makeup is subjective (O'Connell and Wright 1997). We present an objective strategy for binning alleles that tends to preserve the relationships among baseline samples and maintain the inherent ability of the binned data to differentiate populations. Although rare alleles and presumed sampling zeros are not necessarily eliminated, their number tends to be reduced substantially. The performance of the method is illustrated by comparing pairwise measures of genetic distance (Cavalli-Sforza and Edwards (1967) chord distance and F_{ST}), tests of homogeneity, and estimates of mixture composition and population membership between original and binned baseline data of Yukon River chum salmon (*Oncorhynchus keta*) and western Alaska Dolly Varden (*Salvelinus malma*).

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Methods

Notation

Let P denote the number of baseline populations, A be the number of alleles, n_{ij} be the number of alleles of type j observed in a sample from population i, n_i be the total number of alleles observed in a sample from population i, and π_{ij} be the true proportion of alleles in population i that are of type j.

Binning strategy

Baseline data collected from each of P populations contain a certain, fixed, amount of information regarding the genetic differences between the populations. Our fundamental strategy is to bin alleles in a fashion that maintains the degree of population differentiation that remains in the binned data. Specifically, for any two alleles of a particular locus, say alleles k and m, we test the hypothesis of homogeneity across populations (Roff and Bentzen 1989; Raymond and Rousset 1995; Goudet et al. 1996), i.e., that the allele proportions are equal across all populations; H_0: $\pi_{ik} = \pi_{im}$ for all i versus the global alternative H_1: $\pi_{ik} \neq \pi_{im}$ for at least one i. Allele pairs for which the observed data are consistent with H_0 are candidates for binning because they contribute similar information about the observed genetic differences between populations whether as individual alleles or as a single binned allele. Conversely, allele pairs whose sample data are not consistent with H_0 likely provide disparate information that is useful in distinguishing between two or more populations and they should not be binned.

Consider the simplistic example of data from five populations and a locus with eight alleles (Table 1). Alleles 1 through 3 obviously provide important information regarding the genetic relationships among the populations. Alleles 4 and 5 are also informative, but they provide identical information and they could be binned with no loss of information. We would consider alleles 6 through 8 to be rare alleles. These alleles were not all observed in all population samples, presumably because of their rarity rather than their absence. The value of the data on these three alleles is uncertain, and they could probably be binned with other alleles with little loss of information.

Test statistics

Two statistics for testing H_0 are immediately apparent: a likelihood ratio statistic and a Pearson statistic (Agresti 2002). Assuming random association of alleles and random sampling, the observed allele frequencies have a multinomial distribution (Johnson et al. 1997). The full, or unrestricted, likelihood under H_1 is given by

$$L_1 = \prod_{i=1}^{P} \left\{ n_i! \prod_{j=1}^{A} \left(\frac{1}{n_{ij}!} \right) \left(\frac{n_{ij}}{n_i} \right)^{n_{ij}} \right\}$$

while the restricted likelihood under H_0 is

$$L_0 = \prod_{i=1}^{P} \left\{ n_i! \left[\prod_{j=1}^{A} \frac{1}{n_{ij}!} \right] \left[\left(\frac{n_{ik} + n_{im}}{2n_i} \right)^{n_{ik}+n_{im}} \prod_{\substack{j=1 \\ j \neq k,m}}^{A} \left(\frac{n_{ij}}{n_i} \right)^{n_{ij}} \right] \right\}$$

Table 1. Hypothetical allele frequency data observed in samples of 50 diploid individuals from each of five populations.

	Allele								
Population	1	2	3	4	5	6	7	8	Total
1	45	33	9	5	5	1	2	0	100
2	38	24	15	10	10	2	0	1	100
3	63	11	8	8	8	1	1	0	100
4	12	28	45	5	5	0	3	2	100
5	25	49	15	4	4	2	0	1	100

The likelihood ratio test statistic, ψ_{LR}, equals twice the negative log of the ratio L_0/L_1 (Stuart et al. 1999), i.e.,

$$\psi_{LR} = -2\sum_{i=1}^{P} \left\{ n_{ik} \ln\left(\frac{n_{ik} + n_{im}}{2n_{ik}} \right) + n_{im} \ln\left(\frac{n_{ik} + n_{im}}{2n_{im}} \right) \right\}$$

The Pearson test statistic is constructed by determining the number of alleles expected under the two hypotheses. Under H_0, the expected number of allele j in the sample from population i is

$$E[n_{ij}] = \begin{cases} n_{ij} & j \neq k,m \\ \dfrac{n_{ik} + n_{im}}{2} & j = k,m \end{cases}$$

so the usual Pearson χ^2 test statistic, ψ_P, simplifies to

$$\psi_P = \sum_{i=1}^{P} \frac{(n_{ik} - n_{im})^2}{n_{ik} + n_{im}}$$

The asymptotic distribution of both test statistics is a chi-square distribution. However, because of the prevalence of rare alleles and potentially small sample sizes, the observed frequencies will usually be too small to rely on asymptotic distributions, and randomization methods (e.g., Manly 1991; Edgington 1995) are required to evaluate the statistical significance of an observed test statistic. These two test statistics are often competitors and their properties are often similar, though Agresti (2002) states that ψ_P often converges more quickly to a chi-square than ψ_{LR}.

Binning algorithm

Given an original baseline matrix of allele frequency data for P populations and A alleles, the value of the chosen test statistic, either ψ_{LR} or ψ_P but generically denoted ψ here, is computed for all pairs of alleles. Note that all $(n)(n-1)/2$ possible pairs of alleles could be evaluated or, if the alleles were ordered by a measure such as size, only the $(A-1)$ consecutive pairs could be considered. In either case, the data matrix is randomly permuted a large number of times, K, such that the marginal frequencies of the entire $P \times A$ matrix remain fixed; this is the randomization method used for exact tests of contingency table data (Agresti 2002). For each permutation of the matrix, the test statistic is computed for each allele pair and the values obtained, ψ^*, are compared with ψ. The number of times ψ^* equals or exceeds ψ, denoted k, is recorded for each pair of alleles, and the pair having the largest value of k is identified. The ratio $p = k/K$ is an estimate of the significance of an exact test of the hy-

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Table 2. Measures characterizing the chum salmon (*Oncorhynchus keta*) and Dolly Varden (*Salvelinus malma*) data sets used to evaluate the allele-binning algorithm.

Data set	No. of populations	Mean baseline sample size	No. of loci	Expected heterozygosity (H_e)	F_{ST}
Chum salmon	10	90	11	0.504	0.019
Dolly Varden	5	157	6	0.788	0.041

pothesis that the allele proportions are equal across all populations; large values of p indicate that the allele proportions are not statistically different among the populations. If p exceeds a specified threshold, p_{max}, then the two alleles are binned to form a new allele, the number of alleles A is reduced by 1, and the entire process is repeated with the new $P \times A$ data matrix; otherwise the process terminates.

Comparison of original and binned data sets

Two data sets were used to illustrate the effects of binning alleles using this method. The first consists of allele frequency data for 11 loci in 10 populations of chum salmon sampled from the Yukon River drainage (Flannery 2004). These data have moderate polymorphism and a low level of genetic variation (Table 2). The second data set consists of allele frequency data on six loci from five populations of Dolly Varden in western Alaska (Penelope Crane, US Fish and Wildlife Service, Conservation Genetics Laboratory, 1011 E. Tudor Road, Anchorage, AK 99503, USA, unpublished data). The Dolly Varden data have greater polymorphism and a higher level of genetic variation (Table 2). The alleles of each locus of these two data sets were binned using the algorithm previously described, as implemented in a computer program which is available from the authors. All possible allele pairs were considered for binning using the likelihood ratio test statistic, a threshold $p_{max} = 0.10$, and $K = 100\,000$ permutations.

The number of alleles in a data set and the number of alleles with an observed count of zero for some populations were compared before and after binning. In addition, for each locus in each data set, the observed allele frequencies were summed across populations and the proportion of the total comprised of each allele was computed. The proportions were categorized into six proportion ranges based on their magnitude: (0.0, 0.01], (0.01, 0.025], (0.025, 0.05], (0.05, 0.075], (0.075, 0.1], and (0.1, 1.0], where the square bracket denotes inclusion of the boundary value in the range. The percentage of the alleles in each range was computed both before and after binning. In addition, alleles that were binned were jointly classified on the basis of their proportions to summarize the relative prevalence of the alleles that were binned. The percentage of all alleles that were binned in each jointly classified proportion range was computed as a summary measure.

For both the original and the binned data sets, pairwise Cavalli-Sforza and Edwards genetic distances (D_C; Cavalli-Sforza and Edwards 1967) were calculated according to formula 9.15 of Nei (1987) and pairwise F_{ST} was calculated using the method of Weir and Cockerham (1984), as implemented in GENEPOP version 3.3 (Raymond and Rousset 1995). For D_C and F_{ST}, the pairwise distances for the original data sets were plotted against the pairwise distances for the binned data sets to determine if the signature of population differentiation was changed by the binning procedure. Homogeneity among all populations was tested for each locus in the original and binned data sets using exact tests of homogeneity, as implemented in the computer program GENEPOP version 3.3 (Raymond and Rousset 1995), to determine if the power to detect differences among populations had been reduced.

The effect of binning alleles on the performance of MSA was evaluated using the simulation capabilities of SPAM version 3.7 (Debevec et al. 2000; Alaska Department of Fish and Game, Gene Conservation Laboratory, http://www.cf.adfg.state.ak.us/geninfo/research/genetics/software). For each population within each data set, 1000 sets of 400 genotypes were randomly constructed from the observed allele proportions of all loci from that population under the assumption that genotypes were in Hardy–Weinberg equilibrium (e.g., Weir 1990). Each collection of 400 genotypes was treated as a mixed-stock sample and the stock composition of the sample was estimated using the conditional maximum likelihood estimator and a randomly sampled version of the population baseline data (Debevec et al. 2000). Such analyses, somewhat analogous to leave-one-out procedures in classification analyses, are termed 100% simulations and are a useful method of assessing the overall utility of a genetic baseline (e.g., Winans et al. 2004). The root mean squared error (RMSE), i.e., the square root of the sum of the variance and the squared bias, was computed from the 1000 estimates obtained for each population; note that perfect estimation would result in a RMSE of 0. Two simulations were conducted for each data set, one using the maximum likelihood estimator of baseline allele proportions, i.e., the observed ratio of allele frequencies to allele sample size, and one using a Bayesian estimator of baseline allele proportions based on the Dirichlet probability distribution (Johnson et al. 1997; Rannala and Mountain 1997). The RMSE obtained for each population using the binned data set was plotted against that obtained using the original data.

The effect of binning alleles on the accuracy of individual assignment analysis was evaluated using version 1.0.02 of the computer program GeneClass (Cornuet et al. 1999). GeneClass was used to estimate the population membership of each individual in all baseline data sets using the Bayesian likelihood and leave-one-out program options. The proportion of individuals whose population membership was correctly identified was computed both for each population and across all populations in a data set and compared before and after binning.

Results

The binning procedure reduced the total number of alleles by 42% in the chum salmon data set (Table 3) and by 58%

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Table 3. A comparison of the number of alleles, number of alleles with observed counts of zero in some samples, and the significance of exact tests of homogeneity in the original and binned chum salmon (*Oncorhynchus keta*) data sets.

	No. of alleles			No. of alleles with counts of zero			Significance of homogeneity test	
Locus	Original	Binned	Percent reduced	Original	Binned	Percent reduced	Original	Binned
Oke-11	5	4	20	0	0	—	<0.0001	<0.0001
Oke-3	8	5	38	30	6	80	<0.0001	<0.0001
Oke-4	4	2	50	13	0	100	<0.0001	<0.0001
Oke-8	2	2	0	1	1	0	<0.0001	<0.0001
Oki-1L	3	3	0	3	3	0	0.0002	0.0002
Oki-1U	18	9	50	28	7	75	<0.0001	<0.0001
Oki23-1	4	3	25	9	0	100	<0.0001	<0.0001
Ots-103	36	17	53	115	14	88	<0.0001	<0.0001
Ots2-1L	2	2	0	0	0	—	<0.0001	<0.0001
Ots2-1U	5	3	40	14	4	71	0.0001	<0.0001
Ots3-1	15	9	40	62	39	37	<0.0001	<0.0001
Totals	102	59	42	275	74	73		

Table 4. A comparison of the number of alleles, number of alleles with observed counts of zero in some samples, and the significance of exact tests of homogeneity in the original and binned Dolly Varden (*Salvelinus malma*) data sets.

	No. of alleles			No. of alleles with counts of zero			Significance of homogeneity test	
Locus	Original	Binned	Percent reduced	Original	Binned	Percent reduced	Original	Binned
Smm-3	3	2	33	0	0	—	0.0038	0.0011
Smm-10	26	10	62	42	8	81	<0.0001	<0.0001
Smm-17	19	9	53	28	3	89	<0.0001	<0.0001
Smm-21	15	8	47	32	14	56	<0.0001	<0.0001
Smm-22	27	11	59	37	7	81	<0.0001	<0.0001
Smm-24	38	14	63	48	12	75	<0.0001	<0.0001
Totals	128	54	58	187	44	76		

Table 5. The percentage of chum salmon (*Oncorhynchus keta*) alleles in each of six proportion ranges, with square brackets denoting inclusion, before and after binning.

		Allele proportion range						
Allele proportion range	Percent before binning	(0.0, 0.01]	(0.01, 0.025]	(0.025, 0.05]	(0.05, 0.075]	(0.075, 0.1]	(0.1, 1.0]	Percent after binning
(0.0,0.01]	33.3	43.4	15.1	0.0	1.9	1.9	7.5	6.8
(0.01,0.025]	14.7		0.0	7.5	3.8	0.0	3.8	13.6
(0.025,0.05]	15.7			1.9	1.9	0.0	3.8	20.3
(0.05,0.075]	8.8				1.9	0.0	1.9	8.5
(0.075,0.1]	4.9					0.0	0.0	13.6
(0.1,1.0]	22.5						3.8	37.3

Note: Pairs of alleles that were binned are jointly categorized by the proportion of each allele to summarize how alleles of various relative abundances were binned; percentages of the 53 pairs that were binned are presented.

in the Dolly Varden data set (Table 4). The number of alleles with an observed count of zero in some baseline samples was reduced by approximately 75% in both data sets, while the results of exact tests of homogeneity based on the original and binned data sets were essentially identical (Tables 3 and 4). Rare alleles were binned with both other rare alleles and more common alleles in both data sets (Tables 5 and 6). In addition, some common alleles were binned together and some rare alleles appeared too informative to bin (Tables 5 and 6).

In both data sets, D_C decreased slightly for the binned data. The magnitude of change is consistent across the range of observed measures of distance, with all points being located near and slightly below the one-to-one line (Figs. 1*a*,

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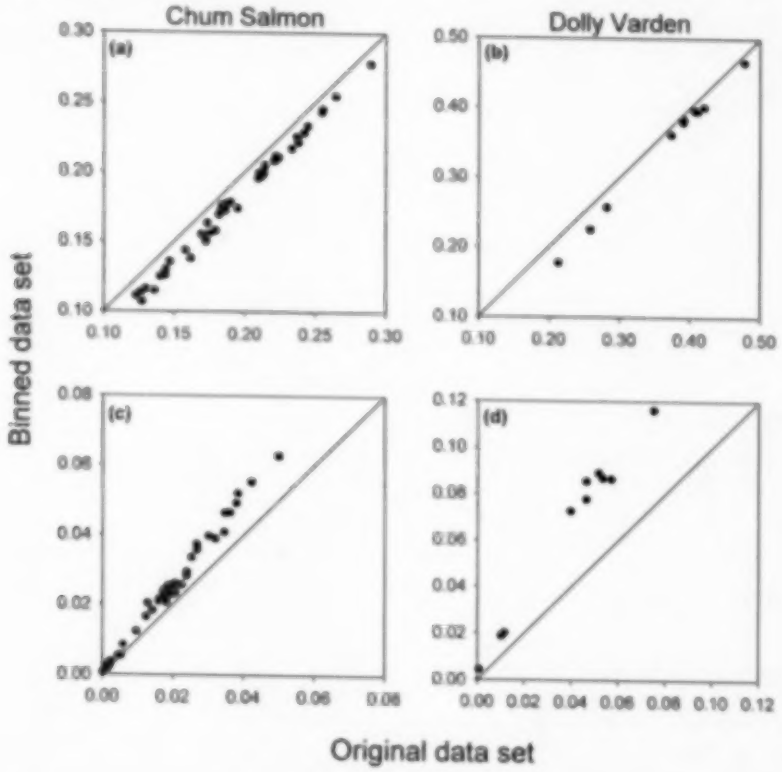
Table 6. The percentage of Dolly Varden (*Salvelinus malma*) alleles in each of six proportion ranges, with square brackets denoting inclusion, before and after binning.

Allele proportion range	Percent before binning	Allele proportion range						Percent after binning
		(0.0, 0.01]	(0.01, 0.025]	(0.025, 0.05]	(0.05, 0.075]	(0.075, 0.1]	(0.1, 1.0]	
(0.0,0.01]	37.5	18.9	14.9	12.2	5.4	2.7	4.1	9.3
(0.01,0.025]	18.8		5.4	5.4	1.4	1.4	5.4	14.8
(0.025,0.05]	17.2			2.7	1.4	9.5	6.8	9.3
(0.05,0.075]	6.3				0.0	1.4	1.4	18.5
(0.075,0.1]	10.2					1.4	0.0	11.1
(0.1,1.0]	10.2						1.4	37.0

Note: Pairs of alleles that were binned are jointly categorized by the proportion of each allele to summarize how alleles of various relative abundances were binned; percentages of the 74 pairs that were binned are presented.

Fig. 1. A comparison of the results of computing Cavalli-Sforza and Edwards (1967) chord distance (D_C; *a* and *b*) and F_{ST} (*c* and *d*) measures of genetic distance for all pairwise combinations of populations with the original and binned chum salmon (*Oncorhynchus keta*) and Dolly Varden (*Salvelinus malma*) data sets.



1b). Pairwise F_{ST} values increased slightly for the binned data, and the magnitude of the increase is positively related to the magnitude of F_{ST} computed with the original data (Figs. 1*c*, 1*d*).

Binning alleles consistently and substantially reduced the RMSE of the conditional maximum likelihood estimates of mixture composition when the maximum likelihood estimator of baseline allele proportions was used (Figs. 2*a*, 2*b*). The majority of the reduction in RMSE was due to a reduction in bias, as there was little difference in estimated standard errors. The RMSE improved less markedly when using the Bayesian estimator of the baseline allele proportions (Figs. 2*c*, 2*d*). In addition, though it is not pertinent to an evaluation of the binning algorithm, it is interesting to note that use of the Bayesian estimator of baseline allele proportions generally led to reduced bias and increased precision with both original and binned data sets.

The accuracy of population membership estimation also improved using the binned data sets. For chum salmon, the proportion of individuals correctly assigned increased from 0.350 to 0.495, while assignment of Dolly Varden improved less markedly, from 0.733 to 0.757. The proportions cor-

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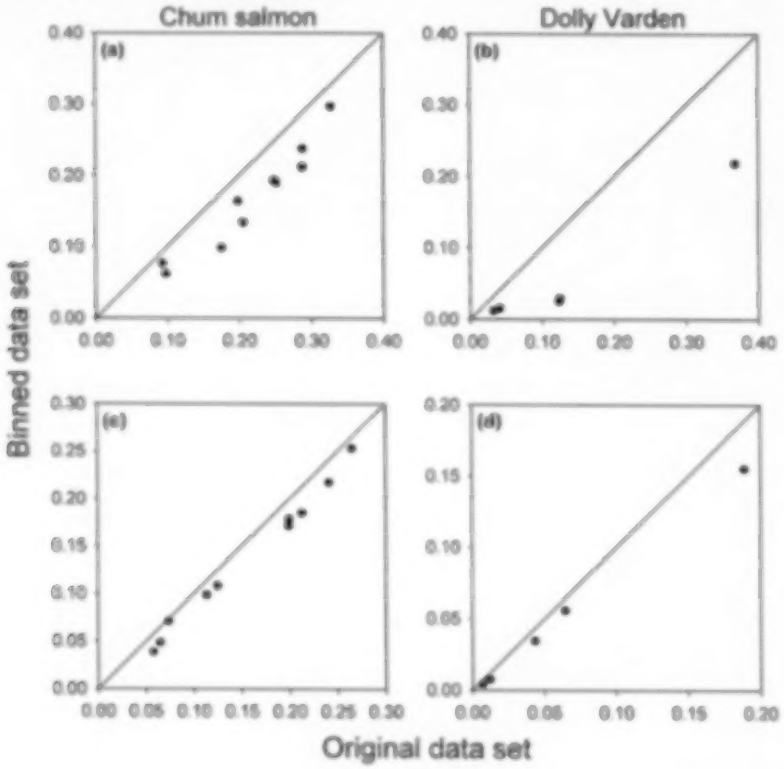
Fig. 2. The root mean square error (RMSE) of conditional maximum likelihood estimates of stock composition using both maximum likelihood (*a* and *b*) and Bayesian (*c* and *d*) estimators of allele proportions for the original and binned chum salmon (*Oncorhynchus keta*) and Dolly Varden (*Salvelinus malma*) data sets. Results are derived from 1000 mixtures comprised of 400 genotypes randomly generated from each individual population (100% simulations).



rectly assigned within individual populations before and after binning are plotted (Fig. 3).

Discussion

Our goal was to develop an objective method to reduce the number of alleles in a data set, particularly rare alleles, while retaining the genetic signature observed among baseline populations. Results from our analyses of these two data sets suggest that our objective was largely met. The total number of alleles and the number of alleles with observed counts of zero were both reduced substantially, with little apparent loss of information. Cavalli-Sforza and Edwards (1967) chord distances decreased, but the decrease was slight and consistent in magnitude among all pairwise combinations of populations. Some decrease was expected because Cavalli-Sforza and Edwards chord distances are larger for loci with greater numbers of alleles (Kalinowski 2002). Because the decrease was relatively slight, we primarily attribute it to a reduction in polymorphism rather than a reduction in power to differentiate between populations, which is consistent with the simulation results. In contrast, the values of F_{ST} computed with the binned data consistently increased. The magnitude of the change appears to be related to the value of F_{ST} computed with the original data, with the binning method leading to greater increases in F_{ST} for populations whose original data had larger values of F_{ST}. Homozygosity influences the maximum value that F_{ST} can attain (Hedrick 1999), and high heterozygosity may lead to negatively biased F_{ST} estimates, particularly for populations separated at larger spatial scales (Kalinowski 2002; Olsen et al. 2004). Heterozygosity decreases when alleles are binned, and rare alleles are more likely to be both binned and associated with heterozygotes, leading to a greater effect of the binning procedure for larger values of F_{ST}.

Binning alleles did not measurably reduce our ability to detect differences in allele composition across populations using an exact test of homogeneity. This result was anticipated given the similarity between the test of homogeneity, using all alleles, and the binning algorithm, which is based on the same test of homogeneity sequentially applied to pairs of alleles. Even so, that we observed essentially no increase in significance levels relative to the original data sets is indicative that the binned data retain the primary characteristics of the original data.

Constrained estimation with conditional maximum likelihood contributes to bias in mixture estimates (Pella and Milner 1987), and options for reducing this bias are limited. Increasing sample sizes of baseline populations can reduce bias but may be costly or otherwise infeasible. Binning al-

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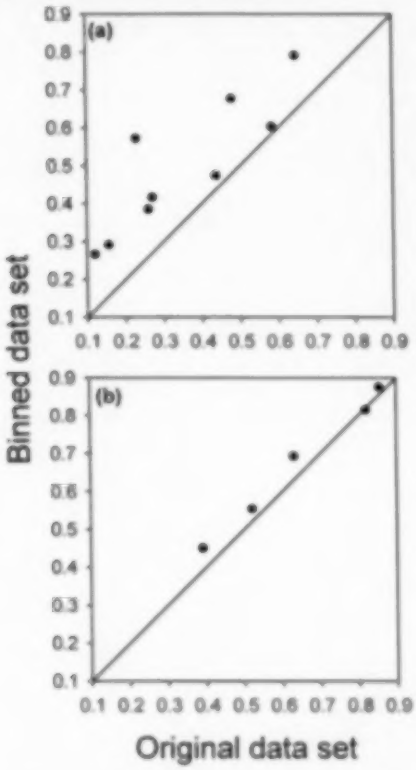
Fig. 3. A comparison of the proportions of individuals of (*a*) chum salmon (*Oncorhynchus keta*) and (*b*) Dolly Varden (*Salvelinus malma*) whose population membership was correctly estimated before and after alleles were binned.



leles increases the precision of allele composition estimates, an effect similar to increasing sample sizes, and our simulation results suggest that binning alleles can lead to a substantial reduction in the RMSE of mixture estimates. Binning alleles reduced the RMSE for all populations in both data sets, primarily through bias reduction, when both estimators of allele composition were used. The reduction in RMSE was markedly greater when the maximum likelihood estimator was used. The comparatively slight reduction in RMSE when the Bayesian estimator was used may not, at first, seem notable. However, if individual populations are pooled into larger groupings using the allocate-sum procedure (Wood et al. 1987), as is common in MSA, the reductions for individual populations would be at least partially additive within the aggregates and could lead to a marked improvement at the group level with some data sets. The combined approach of first binning alleles and then incorporating a Bayesian estimator of baseline allele proportions to reduce the effect of sampling error and rare alleles may be the preferred technique when performing conditional maximum likelihood analyses.

Binning alleles also led to improved accuracy in estimating the population membership of individual fish. As with the MSA results, the cause of the improvement is most likely the increased precision of allele composition estimates and the corresponding reduction in data noise. The substantially greater improvement in accuracy for the chum salmon data set is thought to reflect the lower level of genetic diversity among those populations.

The results indicate that the results of the binning algorithm are fairly complex. Rare alleles were often binned together in both data sets; however, rare alleles were frequently binned with more prevalent alleles and two common alleles were occasionally binned. Rare alleles did not tend to get binned into a single common class of alleles, and some fairly rare alleles appeared to contain too much power to discriminate populations to be binned. This suggests that current methods of binning alleles, or simple approaches such as simply binning all rare alleles into a single allele class, are likely to cause a reduction in power to discriminate populations.

Several avenues for further work in this area are apparent. For example, we have presented two test statistics but have not attempted to investigate which might be preferred. A probability test, e.g., Raymond and Rousset (1995), could provide a third alternative. Simulation studies to compare the performance of these statistics could be used to determine if one statistic is consistently preferable, or if certain statistics have superior properties under certain conditions. Also, we have provided no guidance on the appropriate choice of a p threshold (p_{max}) for terminating the binning process. In our analyses to date, we have generally observed a series of very large p values, leading to allele binning and fewer rare alleles, followed by a sharp reduction to quite small p values. This suggests that the results we obtained are not particularly sensitive to the threshold used. However, selecting a threshold is analogous to selecting a significance level for a statistical test or confidence interval. From that perspective, appropriate values may well depend on characteristics of the data set under consideration, the degree of binning desired, and the preferences of individual researchers. In practice, we recommend trying several values with any particular data set. For example, in applications with many populations covering extremely large geographic areas, such as that of Seeb et al. (2004), use of a small threshold may be necessary to achieve the degree of binning we have obtained. It is possible that only limited binning can be achieved with such large data sets without losing power to differentiate between important subsets of populations. If interest is primarily between groups of populations that can be identified a priori, it may be possible to modify this method so that differentiation between groups is maintained without consideration of differentiation within groups. While we anticipate subsequent work on these and similar issues, we also encourage other researchers to experiment with and refine this approach.

The allele-binning method we have described does not solve all problems associated with use of highly polymorphic loci. In particular, there is no guarantee that all rare alleles will be binned with other alleles. In the examples considered in this work, the number of rare alleles was substantially reduced, but they were not eliminated. If rare alleles remain common after binning, one could bin further using other criteria, though some power to discriminate among populations may be lost. The method also provides no direct guidance on how to handle alleles observed in mixture samples that are absent from all baseline samples. One possibility would be to use this method to bin alleles, order-

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ing alleles based on size and only considering consecutive pairs for binning, and subsequently construct size ranges based on the midpoints between allele bins. Alleles newly observed in a mixture sample would then automatically be placed in the appropriate bin. However, the most straightforward solution would appear to be to bin alleles and then use a Bayesian estimator of allele proportions.

Although we do not necessarily recommend binning alleles in all applications, binning alleles of highly polymorphic loci is a common practice. If alleles are to be binned, the method for constructing bins should be objective and the measure used to guide binning decisions should be directly related to the analytical objectives. Within a MSA framework, the most advantageous allele bins are those that minimize the number of rare alleles and preserve the power to discriminate among populations. That form-follows-function perspective has motivated our approach to this problem, and the method we propose largely meets that ideal. In addition, with the data sets evaluated to date, the statistical properties of conditional maximum likelihood estimates of mixture composition have been improved. Although the method could be modified to produce bins that satisfy other criteria, the power to differentiate between stocks is so fundamental that we expect our method will be robust in many settings. We recommend that other researchers experiment with use of this method, as deemed appropriate, with the goal of increasing the utility of genetic techniques in the study and management of wildlife populations.

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Watershed-level sampling effort requirements for determining riverine fish species composition

Katherine L. Smith and Michael L. Jones

Abstract: Accurate assessments of watershed-level species composition are necessary for comparative ecological studies, ecosystem health assessments, monitoring, and aquatic conservation prioritization. Several studies have addressed sampling effort requirements for characterizing fish species composition at a section of stream, but none have examined watershed-level requirements. In the spring and summer of 2002, we extensively sampled nine Great Lakes watersheds to assess sampling-effort requirements. Sampling requirements increased with the targeted percentage of estimated species richness. Sampling 15–119 randomly selected reaches of stream, stratified by stream order, was on average sufficient to detect 80%–100% of estimated species richness. Watershed size (km^2) and estimated species richness each showed a weak, negative correlation with sampling-effort requirements in our study streams, with Pearson's correlation coefficients of –5.06 and –0.590, respectively. Because of among-watershed variability in sampling effort requirements, field crews should plot species accumulation curves onsite to determine adequate inventory completion. Based on the difficulty of detecting the last 10% of species, random sampling should be conducted in conjunction with targeted sampling of rare species.

Résumé : Des évaluations précises de la composition des espèces à l'échelle du bassin versant sont nécessaires pour les études écologiques comparées, l'évaluation de la santé des écosystèmes, le suivi environnemental et la définition des priorités de conservation aquatique. Plusieurs études ont cherché à déterminer les efforts d'échantillonnage requis pour caractériser la composition spécifique des poissons dans une section de cours d'eau, mais aucune n'a abordé le problème à l'échelle du bassin versant. Au printemps et en été 2002, nous avons fait un important échantillonnage de neuf bassins versants des Grands Lacs afin de déterminer les efforts d'échantillonnage requis. L'échantillonnage requis augmente en fonction du pourcentage de la richesse spécifique estimée que l'on vise à atteindre. L'échantillonnage de 15–119 sections de cours d'eau choisies aléatoirement, stratifiées en fonction de l'ordre du cours d'eau, suffit en moyenne pour détecter respectivement 80 et 100 % de la richesse spécifique estimée. Il existe une corrélation négative faible entre la taille du bassin versant (km^2) et la richesse spécifique estimée, d'une part, et les efforts d'échantillonnage requis dans les cours d'eau étudiés, d'autre part; les coefficients de corrélation de Pearson respectifs sont de –5,06 et de –0,590. Puisque les efforts d'échantillonnage requis varient d'un bassin versant à un autre, les équipes d'inventaire devraient tracer les courbes d'accumulation des espèces pour s'assurer qu'elles ont complété un inventaire adéquat. Comme les derniers 10 % des espèces sont difficiles à obtenir, l'échantillonnage aléatoire devrait s'accompagner d'un échantillonnage ciblé des espèces rares.

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Introduction

Increasing concern for the conservation of biological diversity necessitates the development of practical tools that can be used to determine the species composition of threatened habitats. Conservation concerns are pressing for freshwater fish: in the US alone, 37% of freshwater species are at risk for extinction (Braun et al. 2000). Sound research and conservation actions are dependent on adequate knowledge of species composition and distribution. Sampling-effort guidelines for determining species composition are essential to this goal. However, studies to develop sampling-effort guidelines for riverine fish species inventories have targeted the stream-reach level rather than entire watersheds (Lyons 1992; Peterson and Rabeni 1995; Patton et al. 2000). Such reach-level inventories are not reliable for characterizing fish assemblages of entire watersheds due to between-site heterogeneity.

Guidelines for watershed-level fish surveys are urgently needed. Most stream fish research is currently targeted at small-scale processes; however, reach-level research is often inadequate to address watershed-level threats (Fausch et al.

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K.L. Smith[1,2] and M.L. Jones. Department of Fisheries and Wildlife, 13 Natural Resources Building, Michigan State University, East Lansing, MI 48824, USA.

[1]Corresponding author (e-mail: smithkat@uga.edu).
[2]Present address: Institute of Ecology, University of Georgia, Athens, GA 30602, USA.

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2002). For many riverine fishes, remarkably little is known about the extent of their movements during their entire life (Minns 1995). Fish may move throughout the watershed to reach critical habitats at different life stages, suggesting that a larger scale of observation may be appropriate when assessing species composition for the purposes of conservation. Stream fish species are particularly vulnerable to degradations of their habitat (Williams et al. 1989). Habitat destruction occurs at a variety of scales, but is widespread at the watershed-scale from threats including land-use change and water withdrawals (Richter et al. 1997). In addition, local habitat manipulations can have large-scale effects, particularly if they create impediments to fish movement. For example, downstream watershed development projects, such as dams, may affect headwater species (Winston and Taylor 1991; Pringle 1997; Fairchild et al. 1998). In the Laurentian Great Lakes basin, this issue has arisen because the Great Lakes Fishery Commission is considering expanding its use of low-head barrier dams to prevent exotic sea lamprey (*Petromyzon marinus*) from accessing riverine spawning habitats. Knowledge of the species composition of the entire watershed is necessary to assess the potential effects of such habitat manipulations.

No survey design can ensure detection of all species present in an area, so determining an appropriate trade-off between the risk of failing to detect species and wasting resources via excessive sampling effort is necessary. The level of completion required for an inventory will depend on research or management objectives. For some community-level research, detecting the rarest species is critical, whereas for other purposes, such as environmental assessments, detailed knowledge of community composition may not be essential (Angermeier and Karr 1986; Vernhes and Younes 1993; Cao et al. 1998). Conservation resources are often allocated to watersheds with the greatest apparent number of species (Rutledge et al. 2001). Ignoring the effects of sampling effort on estimates of species richness may result in overemphasis of conservation resources to watersheds that have experienced greater sampling effort and have larger detected, rather than true, species richness. For example, Nelson et al. (1990) found that areas of relatively high endemic species were strongly correlated with sampling intensity. Sampling effort guidelines are needed to develop accurate, efficient sampling protocols and best allocate limited resources.

Species accumulation curves have been used to guide landscape-level species inventories and to develop sampling guidelines for a variety of taxa, including plants (Gimaret-Carpentier et al. 1998), birds (Neave et al. 1997), insects (Dobyns 1997), and algae (Hellmann and Fowler 1999; Moreno and Halffter 2000). Species accumulation curves describe the positive, monotonic, asymptotic relationship between sampling effort and number of species detected in an inventory. This pattern occurs because many species are found in the first samples, whereas additional sampling yields a decreasing number of new species. Species accumulation curves provide a quantitative method for assessing the completeness of faunal inventories, estimating total species richness, and developing guidelines for the minimum sampling effort needed to reach a target level of inventory completeness (Moreno and Halffter 2001). This information is particularly important at the watershed level, where species inventories can be very costly.

The shape of a species-accumulation curve depends on the relative abundance and distribution of species, so the best mathematical model to describe the curve will depend on the taxa, environment, and scale (Colwell and Coddington 1994). Because a single model cannot best fit all taxa and environments, Colwell and Coddington (1994) suggested testing several models. The model that best fits the observed data should be selected to characterize the relationship between sampling effort and number of species detected. Few studies have conducted such a model intercomparison (Flather 1996), and none have been completed for fish species inventories. Choosing an appropriate model is essential for accurately assessing the completeness of species inventories and developing sampling-effort guidelines.

In this study, we surveyed nine small- to medium-sized watersheds in the Laurentian Great Lakes basin to determine watershed-scale fish species composition. We used these data to accomplish the following: (*i*) determine the best model to describe fish species accumulation at the watershed level; (*ii*) quantify the sampling effort needed to characterize species composition at the watershed level; (*iii*) examine the effects of model choice on estimates of sampling-effort requirements; and (*iv*) determine if physical characteristics of our watersheds were correlated with sampling-effort requirements.

Methods

Study sites

We selected nine Great Lakes watersheds that differed in location within the basin, physical characteristics, and fish community types (Fig. 1). Watershed areas ranged from 23.6 to 432.8 km^2, and streams were third to fifth order at their mouths. Six of the nine streams were shallow enough to be sampled with a backpack electrofisher at all locations, while the three largest streams required the use of a boat shocker. In this analysis, we examined only wadeable (first through third order) sections of the watershed to facilitate comparisons among streams. Fish assemblages ranged from highly diverse cold–cool–warm water communities (>60 species) to low-diversity coldwater communities (<20 species).

Sampling locations

All streams were delineated into separate first- to fifth-order sections of stream using topographical maps with a 1:50 000 scale according to the Strahler method (Strahler 1957). To ensure proportional representation, we grouped sections of stream by order and subdivided long sections so they were not underrepresented in the selection process. A minimum of six sections was randomly selected from each stream order group (i.e., first, second, and third order). Within each selected section, we determined all access points from the map and, using a random number generator, randomly selected one access point at which to conduct sampling. Lyons (1992) recommended sampling a length of 30 times the mean stream width to characterize fish communities at the reach level in warm-water Wisconsin streams. We adopted this strategy, and at each access point, sampled a

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Fig. 1. Map of Great Lakes watersheds surveyed to determine sampling-effort requirements for assessing fish species composition.

reach of stream that was 30 mean stream widths in length. Wadeable reaches ranged from less than 1 to 28 m wide, and we sampled 20–39 reaches per stream. To account for seasonal variability in species composition, all watersheds included a spring (May and June) and summer (July and August) sampling period. We sampled an equal number of reaches from each stream order group to ensure sufficient representation of all areas of the watershed.

Sampling

We sampled wadeable reaches by backpack electrofishing (Smith-Root® Model 12-B; Smith-Root Inc., Vancouver, Washington). To maximize capture efficiency, we tested and adjusted settings outside the sampling site. Given our study objectives of efficient assessment of species composition, sampling consisted of a single pass. Block nets appear to have little effect on species detection in similar-sized Wisconsin stream reaches over 35 stream widths (Simonson and Lyons 1995), so we did not use block nets. A three-person field crew conducted sampling in an upstream direction, wading back and forth across the stream while moving the anode in a continuous "m" pattern. The entire reach was sampled, with sampling effort proportional to the catch rates of fish in each habitat type. Captured fish were held in large containers for identification and later released. Fish that could not be identified with certainty in the field were preserved in a 10% formaldehyde solution and returned to the lab, where experienced ichthyologists confirmed their identity. Lamprey species were excluded from our analysis because of concerns over field identification of larval lampreys.

Statistical methods

We developed a Monte Carlo simulation program to generate species accumulation curves for each watershed from the species captured at each sampling location. Randomization of sample order is needed for organisms such as fishes that are patchily distributed (Flather 1996) to prevent heterogeneity among samples, and the order in which samples were collected from affecting the curve shape (Reynolds 1996). To generate a curve, we randomly chose one permutation of the sequence of all reaches (samples) without replacement and recorded the cumulative number of species found versus the number of reaches sampled. We repeated this process 1000 times to calculate the average cumulative number of species found per the number of reaches sampled.

Three methods have been used for species richness estimation from inventory data: (*i*) extrapolation from species accumulation curves; (*ii*) nonparametric methods based on species distributions among samples; and (*iii*) parametric models of relative abundance (Palmer 1990; Colwell and Coddington 1994; Walther and Martin 2001). Nonparametric methods are recommended most often for estimation of species richness, because the estimated asymptote and slope of species-accumulation curves differ depending on species abundance patterns (Palmer 1990; Soberon and Llorente 1993; Gomez de Silva and Medellin 2001). Most estimators will underestimate species richness for small sample sizes, and no estimator is universally accepted as best. However, the first-order jackknife technique is often recommended as one of the least biased and most precise estimators (Palmer 1990; Boulinier et al. 1998; Hellmann and Fowler 1999). This technique estimates species richness S_{est} as a function

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Table 1. Description of mathematical models used to characterize species-accumulation patterns in Great Lakes watersheds.

Model	Function	Parameters	Asymptote
1	$S = AX/(1 + BX)$	2	Yes
2	$S = AX^B$	2	Yes
3	$S = A + B\log X$	2	Yes
4	$S = A/(1 + BX^{-C})$	3	No
5	$S = AX^{BEC}$	3	No
6	$S = (A + BX)/(1 + CX)$	3	No
7	$S = (A/B)(1 - e^{CX})$	3	No
8	$S = A(1 - e^{-BX-C})$	3	Yes
9	$S = A(1 - e^{-BX})^C$	3	Yes
10	$S = A(1 - (1 + (X/B)^C)^{-D})$	4	Yes
11	$S = A(1 - e^{-(BX)^{-C}})^D)$	4	Yes

Note: All models exhibit a general nonsigmoidal increasing shape and are described in Ratkowsky (1990) or Flather (1996). S, the number of species detected; X, the number of reaches sampled; A, B, C, and D, parameters.

of the number of observed species S_{obs}, the number of species found in only one sample r, and the number of samples taken n as

$$(1) \qquad S_{est} = S_{obs} + r(n - 1)/n$$

We used this technique to calculate the estimated species richness (S_{est}) from our data. We then determined the percentage of S_{est} actually observed (S_{obs}) in each survey as S_{obs}/S_{est}.

We tested several plausible models to determine the model that best characterized the species-accumulation pattern observed in our watersheds. We compared 11 nonlinear models (Table 1) commonly used in the ecological and species inventory literature (Soberon and Llorente 1993; Colwell and Coddington 1994; Flather 1996). Models were fit with AD Model Builder (Version 6.0.2, Otter Research Limited, Sidney, British Columbia) using a maximum likelihood technique. We compared among models using corrected Akaike's Information Criterion (AIC), which ranks candidate models according to how well they describe the data and parsimony. Corrected AIC takes the form

$$(2) \qquad \text{AIC} = -2\log(\ell(\Theta|y)) + 2K$$

where $\log(\ell(\Theta|y))$ is the estimated log-likelihood of the parameter given the data, and $2K$ is a penalty function for additional model parameters K. This method allows for simple comparison among non-nested models with differing numbers of parameters and is appropriate for ecological data (Burnham and Anderson 2002). For each watershed, each model was given a rank of 1–11 from best (a rank of 1) to worst (a rank of 11) based on its corrected AIC value. The average rank and range of rank was then calculated for each model. To assess possible problems with the use of these models to extrapolate sampling-effort requirements that exceeded our range of observation, we also examined plots of residuals versus sampling effort for each watershed and model. Strong trending of residuals as sampling effort increased toward the maximum observed values would raise concerns about extrapolation.

Table 2. Observed and estimated species richness of Great Lakes watersheds in the spring and summer of 2003.

Watershed	S_{obs}	S_{est}	SE of S_{est}	Reaches
Au Gres	55	57.9	2.7	39
Little Pigeon	32	35.9	3.3	28
Harlow	18	22.8	7.7	25
Sucker	21	22.9	1.8	33
Big Otter	24	28.8	4.0	30
Boyne	30	35.7	9.6	20
Conneaut	35	39.8	5.5	22
Raccoon	25	29.8	5.9	22
Grindstone	34	38.8	3.7	23

Note: Columns from left to right indicate the number of species observed (S_{obs}) and estimated (S_{est}), the standard error (SE) of the estimate of S_{est}, and the total number of reaches sampled (Reaches) per watershed.

Using the model that best fit the data for each watershed, we estimated the amount of sampling effort, presented as number of reaches, necessary to detect 80%, 90%, 95%, and 100% of S_{est} in each watershed. We were able to use our observed species-accumulation pattern to determine the average number of reaches necessary to detect 80% of S_{est} in all watersheds. For some watersheds, extrapolating beyond the range of our observations to estimate sampling-effort requirements for detecting greater than 80% of S_{est} was necessary.

Different models may fit the data reasonably well, but when extrapolation is required, they may make very different predictions of sampling-effort requirements (Soberon and Llorente 1993). Therefore, we selected the three best models and compared their predictions of sampling-effort requirements. In addition to the choice of a model, the choice of species richness estimator may affect sampling effort estimates. To examine the effect of species-richness estimator choice, we compared sampling effort estimates derived by using each model's projected asymptote (A) to estimates obtained with the first-order jackknife estimator of species richness (S_{est}).

We conducted bivariate correlations (SYSTAT® Version 8.0; SYSTAT Software Inc., Point Richmond, California) to examine the relationship of both watershed size (km^2) and S_{est} to sampling-effort requirements. We considered two measures of sampling effort requirements: (*i*) the number of reaches and (*ii*) the area of stream (measured as number of reaches × average area of stream per reach) needed to detect 80% of S_{est}.

Results

We observed between 18 and 55 species in our nine study watersheds. The observed number of species ranged from 78% to 95% of S_{est} (Table 2). As reflected in percentage of S_{est} detected, species accumulation curves more nearly reached an asymptote in some watersheds than others (Fig. 2). We excluded two watersheds (Harlow and Boyne) from our analysis of sampling-effort requirements because too few reaches were sampled to obtain confident estimates of species richness. The standard errors in S_{est} were particularly high, and less than 80% of S_{est} was detected in both of these watersheds. This increased our uncertainty about the true

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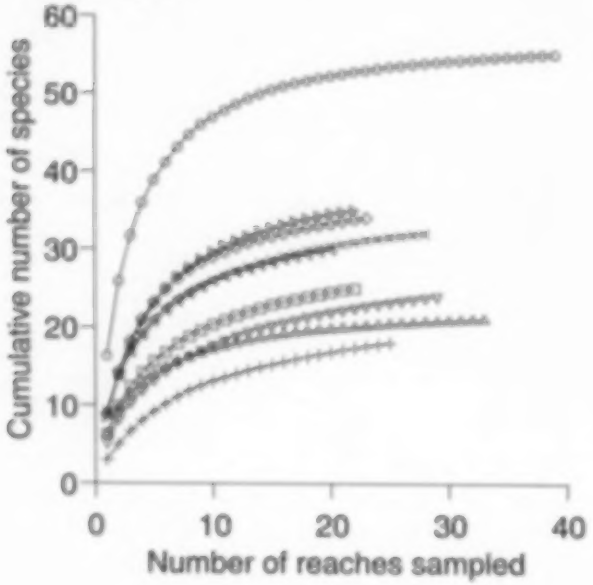
Fig. 2. Species-accumulation curves for nine Great Lakes watersheds: ○, Au Gres; ×, Little Pigeon; +, Harlow; △, Sucker; ▽, Big Otter; ◀, Boyne; ▷, Connean; □, Raccoon; ◇, Grindstone. The cumulative number of species is plotted against the number of reaches sampled.



pattern of species accumulation, leading to poor model fit and potentially biased estimated of sampling-effort requirements. Excluding these two watersheds, the standard error of S_{est} ranged from 1.8 to 5.9 species.

Of the 11 models considered in our analysis, two-parameter models generally fit the data poorly, whereas three- and four-parameter models (models 6, 10, and 11) best fit the data according to the corrected AIC values across all watersheds (Table 3). Model 11 was the best fit (lowest corrected AIC value) for five of the seven watersheds, whereas model 10 was best for the remaining two watersheds. In the two cases in which model 10 was best, model 10 fit the data much better than the second-best model, as indicated by the differences between corrected AIC values (Table 3). Model 6 was the second- or third-best fit for all watersheds, but always had a substantially higher corrected AIC value than the best-fit model. In an examination of residuals plotted against sampling effort, models 11, 10, and 6 consistently showed less trending than the other models we examined.

Within the range of our data, the best three models produced similar estimates of sampling effort requirements (e.g., number of reaches needed to obtain 80% of S_{est}). However, for extrapolation beyond the range of the data (e.g., 95%–100% S_{est}) model 11 consistently produced higher estimates than did models 10 or 6, which predicted very similar estimates to one another (Table 4). Furthermore, the asymptote of model 11 was less than that of S_{est} in all but one watershed, so it could not be used to estimate the number of reaches needed to find 100% of S_{est} for most watersheds.

We used the best model for each watershed to estimate the sampling effort required to detect 80%, 90%, and 95% of S_{est} (Table 4). A sample size of between 9 and 25 reaches (average = 15.1) was needed to detect 80% of S_{est}. To detect 90% of S_{est} the estimate ranged from 17 to 49 (average = 30). To find 95% of S_{est}, between 30 and 98 reaches (average = 49) should be sampled. The Au Gres and Big Otter watersheds always produced the most extreme low and high estimates of sampling effort requirements, respectively. Excluding these watersheds, estimates of sampling requirements to detect 80%, 90%, and 95% of S_{est} were very similar between watersheds, only differing by 5, 7, and 12 reaches, respectively, (Fig. 3).

To determine sampling effort requirements for 100% of S_{est}, we used model 10 for all watersheds. We did not use model 11 because its estimated asymptote was lower than that of S_{est} for several watersheds. Using model 10, the number of reaches needed to detect 100% of S_{est} could be estimated for all watersheds except the Raccoon. We estimated that between 76 and 151 reaches (average = 119) should be sampled to determine 100% of S_{est}.

The choice of species-richness estimator had a smaller effect than model choice on estimates of sampling effort required to achieve a high level (95%) of S_{est}. The average difference in sampling-effort estimates obtained using two different species-richness estimators, the jackknife (S_{est}) or asymptote (A), was less than the difference between estimates from models 10 and 11 for five of six watersheds (Table 5). Grindstone could not be used in this analysis because its species-accumulation curve reached an asymptote lower than the value of S_{est}.

River characteristics were not clearly related to sampling-effort requirements. Watershed size (km^2) and estimated species richness each showed a weak, negative correlation (r = –0.506 and 0.590, respectively; n = 7) with the number of reaches needed to detect 80% of S_{est}. Visual inspection of the data suggested negative relationships (Fig. 4), particularly if the Big Otter River was considered an outlier. Excluding the Big Otter, the correlation between watershed size and number of reaches increased to –0.889. On the other hand, when area of stream was used as the measure of effort requirement, the relationships appeared weakly positive (Fig. 4), but were not significant even with the Big Otter River excluded.

Discussion

This study provides an empirical basis for estimating watershed-level sampling-effort requirements, and our results from seven watersheds provide rough guidelines for sampling-effort requirements to assess fish species composition in moderately sized watersheds in the Great Lakes basin. We believe our sampling was adequate to support our findings: two watersheds that we judged to be insufficiently sampled were excluded from our analysis, and species-accumulation curves for the remaining seven watersheds were approaching an asymptote, minimizing the chance for biases in our jackknife estimates of species richness (Palmer 1990; Hellmann and Fowler 1999). The watersheds we surveyed include a broad range of physiographic and zoogeographic characteristics, with estimated species richness ranging from 20 to 60 species. We conclude that our findings should have broad applicability to this region, and perhaps even to other regions where stream habitat conditions

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Table 3. Model fit results for riverine fish species-accumulation curves in Great Lakes Watersheds.

	Model										
Watershed	1	2	3	4	5	6	7	8	9	10	11
Au Gres	185.7	141.4	106.3	229.5	201.2	–45.7	–17.9	5.4	–36.3	–81.9	–11.2
Little Pigeon	110.7	56.1	4.8	100.7	35.1	–55.0	–14.0	51.9	–31.3	–59.3	–92.3
Sucker	104.6	49.2	0.4	107.4	57.8	–90.3	–58.4	12.1	–70.9	–96.2	–132.0
Big Otter	95.2	37.6	–29.7	84.0	36.2	–94.3	–28.6	44.4	–38.5	–111.0	–127.0
Conneaut	70.5	38.4	9.8	85.9	32.7	–57.9	–40.9	–5.3	–28.6	–55.5	–71.2
Raccoon	66.3	18.9	–29.6	57.1	9.8	–47.6	29.2	27.9	–26.5	–55.3	–61.5
Grindstone	71.9	165.4	30.7	95.2	54.9	–35.1	–34.7	–37.3	–35.5	–51.2	–13.9
Average of Ranks	10.1	8.7	6.0	10.4	8.0	2.6	4.9	6.7	4.1	1.9	2.9
Range of Ranks	9–11	8–11	4–7	10–11	7–10	2–4	4–6	2–9	3–6	1–3	1–6

Note: Corrected Akaike's Information Criterion (AIC) values are a maximum likelihood estimate of model fit corrected for the number of parameters. A lower number indicates a better model (e.g., larger negative values indicate best fit). Average rank and range of ranks for each model and watershed based on corrected AIC values are presented in the last two rows.

Table 4. The number of reaches estimated by models 11, 10, and 6 to obtain 80%–100% of estimated fish species richness (S_{est}) in Great Lakes watersheds.

		Model tested											
		80% S_{est}			90% S_{est}			95% S_{est}			100% S_{est}		
Watershed	Best Model	11	10	6	11	10	6	11	10	6	11	10	6
Au Gres	10	9	9	9	17	17	17	30	30	30	N	151	98
Little Pigeon	11	15	15	15	30	29	29	53	47	44	N	95	76
Sucker	11	13	13	14	28	28	28	60	49	46	200+	147	105
Big Otter	11	25	25	25	49	46	45	98	70	62	N	129	94
Conneaut	11	13	13	13	26	25	25	59	39	38	N	76	71
Raccoon	11	17	17	18	34	33	31	65	54	43	N	200+	65
Grindstone	10	14	14	14	33	29	30	N	50	63	N	118	200+
Average	—	15.1	15.1	15.4	31	29.6	29.3	60.8	48.4	46.6	N	119	84.83

Note: The best model (lowest Akaike's Information Criterion (AIC) model) for each watershed is listed in column two. N indicates that sampling-effort requirements could not be estimated because the model reached an asymptote lower than estimated species richness S_{est}. Likewise, 200+ indicates a very high and unrealistic estimate of sampling requirements.

Fig. 3. Sampling-effort requirements to achieve a targeted percentage of estimated species richness (S_{est}) in Great Lakes watersheds. The amount and range of sampling effort, in reaches, needed to detect 80%, 90%, 95%, and 100% of S_{est} is presented for seven study watersheds.

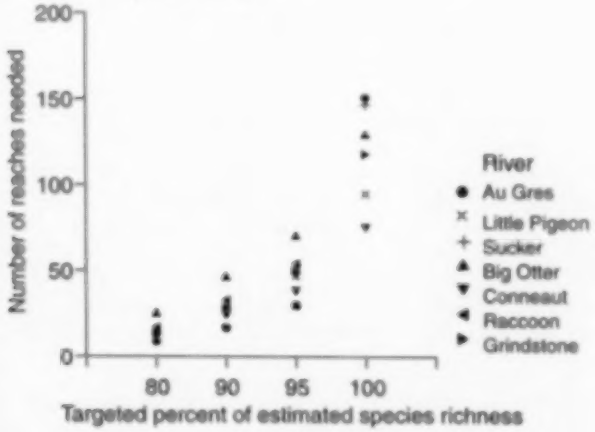

Table 5. Relative influence of species richness estimator and model choice on estimates of sampling-effort requirements for fish species inventories in Great Lakes watersheds.

Watershed	A versus J	10 versus 11
Au Gres	–2	–6
Little Pigeon	15.5	–22.5
Sucker	–2	–14
Boyne	10	–23
Conneaut	9.5	–19.5
Raccoon	–11	–3

Note: The table compares the difference (in number of reaches required to detect 95% of estimated species richness (S_{est})) produced using two methods of estimating species richness (the jackknife estimator (J) and the asymptotic estimator (A) of species richness) to the difference between using models 10 and 11. Grindstone could not be used in this analysis because model 11 produced an asymptote lower than the jackknife value of S_{est}.

are similar and fish species richness lies within a similar range.

Based on our data, extrapolation was necessary to estimate sampling requirements to capture more than 80%–90%

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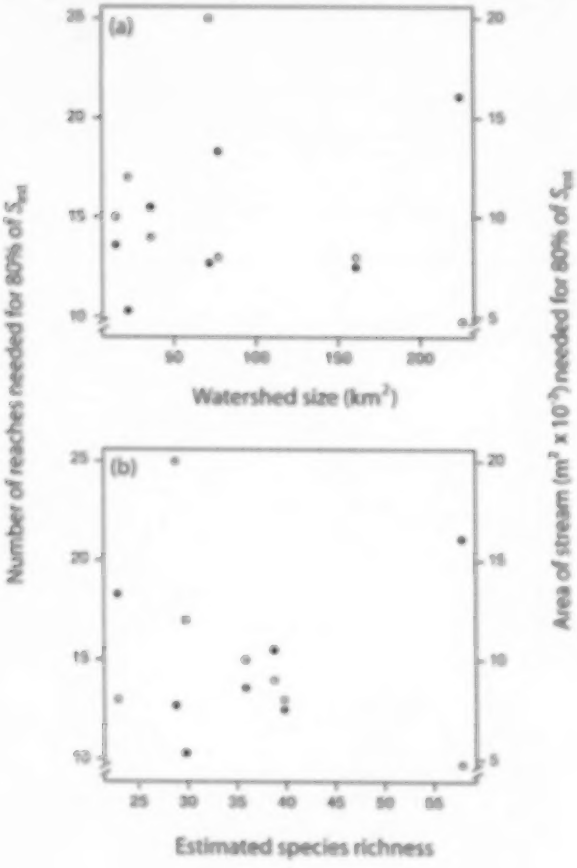
Fig. 4. Scatter plot of (*a*) watershed size versus sampling-effort requirements and (*b*) species richness versus sampling-effort requirements in seven Great Lakes watersheds. Sampling effort is represented as the number of reaches (○) and area of stream (●) needed to detect 80% of estimated species richness (S_{est}). When the number of reaches is used to represent sampling effort, the data suggest a negative relationship between sampling effort and both watershed size and species richness, particularly if the Big Otter is considered an outlier. However, when area of stream is used as a measure of effort, the relationship is weakly positive.


(a)
(b)
Number of reaches needed for 80% of S_{est}
Area of stream ($m^2 \times 10^{-3}$) needed for 80% of S_{est}
Watershed size (km^2)
Estimated species richness

of the species in a watershed. Extrapolation from any model is risky; however, extrapolation from species-accumulation curves has worked well for determining sampling requirements in previous studies (Lyons 1992; Bowen and Freeman 1998; Moreno and Halffter 2000). We found that, on average, 15, 29, 49, and 119 randomly selected reaches of stream, stratified by order, should be sampled to detect 80%, 90%, 95%, and 100% of S_{est}, respectively. Based on our field time records, to achieve these levels of S_{est}, a three-person crew would need to sample for an average of 3, 5, 9, and 20 field days, respectively. The variability among watersheds in effort requirements was fairly large, and increased with the target percentage of S_{est}. This among-watershed variability implies that our average sampling-effort requirements should be viewed as guidelines for planning, rather than rules. Sampling time will also vary among watersheds as a result of travel time, stream access, crew experience, and watershed size. Target sample sizes should be adjusted during the actual survey by plotting species-accumulation curves as the data are being collected.

In our study, watershed size and species richness were not highly correlated with sampling effort requirements, suggesting that environmental factors are not useful in predicting sampling-effort requirements, based on our small sample size. Visual inspection of the data, however, suggested a negative relationship between sampling effort and both watershed size and species richness, particularly if the Big Otter River is treated as an outlier. Au Gres, the largest watershed, required the fewest reaches to detect 80%, 90%, and 95% of S_{est}. The relationship between watershed size and sampling effort, however, depends on the definition of sampling effort used. In our analysis, using area of stream rather than number of reaches eliminated the negative correlation between watershed size and sampling effort. Results from other studies have also been equivocal; some studies have found that stream width is not correlated with sampling effort requirements (Lyons 1992; Hughes et al. 2002), while Paller (1995) found a negative relationship between channel size and sampling-effort requirements. In our case, the lack of a significant relationship may be a result of the low statistical power involved in a study of only seven watersheds. Future studies should further examine the possibility of a negative relationship between sampling effort and watershed size or species richness.

While sampling effort was poorly correlated with species richness of the watershed, it is likely related to patchiness in species distribution. A watershed with many rare species or species only associated with a particular habitat would likely require greater sampling effort than a watershed where species are more evenly distributed. Landscape factors affecting species distribution should also be considered in sampling design and in future studies. For example, few species may occur in reaches above high waterfalls, potentially reducing the effectiveness of extensive sampling in these areas.

Good model fit and knowledge of the system are necessary for choosing an appropriate model for extrapolation. Comparing the fit of several models improved our ability to accurately estimate sampling-effort requirements. For example, we found that two-parameter models provide a poor fit to the data and often exhibit biases at the extremes of the curves. Bias, particularly at the extreme of the data range, may result in considerable overestimates when extrapolating sampling-effort requirements to detect a high percentage of S_{est}. Many models used in species inventory studies have demonstrated such biases (Soberon and Llorente 1993).

In a comparison of models to characterize species-accumulation curves for breeding bird surveys, Flather (1996) found models 11 and 10 to be the first- and second-best fit, respectively, based on average rank. Of the models we tested, we found model 10 to be the best model for extrapolating sampling-effort requirements from species-accumulation curves for stream fish. Although model 10 provided the best fit for only two of the seven watersheds, it had the best overall performance with an average rank of 1.9, and was at worst the third-best model. Model 11, the best fit for five of

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seven watersheds, ranked as low as sixth for the other two watersheds. In addition, model 11 reached an asymptote very rapidly, and its asymptote parameter was often less than S_{est}. As a result, model 11 could not be used to estimate sampling-effort requirements for 100% of S_{est}, and often produced estimates for <100% of S_{est} that appeared unreasonably high upon visual inspection of species-accumulation curves.

Species-accumulation curves provide a method for quantitative assessment of faunal inventories (Soberon and Llorente 1993; Colwell and Coddington 1994), which allows measurement of the percentage of species detected, development of sampling-effort guidelines, and comparisons among watersheds. The use of species-accumulation curves for species inventories is widely accepted; however, there are several limitations to the effectiveness of this technique. No one species-richness estimator or model to characterize curves is universally accepted as best (Bunge and Fitzpatrick 1993). Although the first-order jackknife estimator has performed well in many studies (Palmer 1990; Hellmann and Fowler 1999), ensuring that it is the best estimator without knowing the true species richness of a watershed is not possible. Future studies should examine the performance of many species-richness estimators for estimating reach and watershed-level species richness. Sampling-effort estimates from model 10, on average the model of best fit, appeared reasonable; however, the model selected to best fit a species-accumulation curve cannot be guaranteed as the best model for extrapolation. We found that the use of a different estimator had a smaller effect on sampling-effort estimates than varying the model choice, which indicates that model choice may be a more important factor in developing sampling-effort guidelines.

Even with proper guidelines and extensive sampling effort, ensuring that all species in a large area have been detected is not possible (Remsen 1994). This concern is especially relevant in streams where fish species are patchily distributed (Angermeier and Smogor 1995), and rare species may only be located in one small area of the watershed. Extremely rare species might only be detected in a standardized protocol if their specific habitats happen by chance to be randomly selected or if their habitats are specifically targeted. Given the impossibility of proving the absence of rare species (Cam et al. 2000), it may be prudent to assume that a species of concern is present in the watershed if it is known to occur in the surrounding region or to conduct targeted sampling for these species.

Techniques of species-richness estimation and modeling of species-accumulation curves are only valid for assessing survey completeness for the seasons or years sampled and for the species that are susceptible to the sampling methods and gears used. Although electrofishing is considered the least biased and most efficient sampling method for stream fishes, it is inefficient for detecting some cryptic fishes (Reynolds 1996; Quinn and Kwak 2003). Species that are unsusceptible to electrofishing will be unaccounted for if this technique is used. In addition, species that are transient occupants of the watershed (e.g., during spawning runs) would not be detected by most standardized sampling protocols. Targeting rare species, species that use the stream on only a seasonal or annual basis, or species not susceptible to electrofishing, may improve detection and increase the rate of species accumulation (Conroy and Noon 1996), but at the cost of inventory standardization.

Improving the allocation of sampling effort may reduce sampling requirements without affecting inventory completeness. For example, the length of reach sampled will affect the number of reaches required to detect a targeted percentage of S_{est}. We chose a reach length of 30 stream widths based on the literature; however, inventory efficiency might be improved by altering the length of reach sampled. In addition, improving the allocation of sampling effort between stream-order strata may further increase inventory efficiency. Future studies of watershed-level sampling-effort requirements should address allocation of sampling effort, rates of species accumulation in larger, higher order watersheds, effects of multiple gear types on effort requirements, and effects of additional seasonal sampling and multiple-year sampling on rates and patterns of species accumulation.

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Population genetics of northern pike (*Esox lucius*) introduced into Lake Davis, California

Andres Aguilar, James D. Banks, Kenneth F. Levine, and Robert K. Wayne

Abstract: We used molecular genetic techniques to identify the source population of northern pike (*Esox lucius*) illegally introduced into Lake Davis, California, and to study the dynamics of genetic change since the introduction. We typed 10 tetranucleotide microsatellite loci from 11 populations and used measures of population differentiation, phylogenetic analysis, and assignment tests to determine the origins of the pre- and post-rotenone-treatment populations. We found that levels of genetic differentiation were low between the pre- and both post-treatment Lake Davis samples and phylogenetic analysis revealed that they were all closely related. Assignment tests classified a high proportion of posttreatment individuals to the original Lake Davis population. Consequently, our results indicate that the fish population that reappeared in 1999 and a subsequent sample in 2002 were descendents or survivors of the initial population. We were unable to assign the pre- or post-treatment individuals consistently to any one population from a panel of potential source populations, indicating that the ultimate source of the Lake Davis population was likely not sampled. Genetic signatures of a recent population bottleneck are evident in the samples from Lake Davis and the effective population size over the sampling period was approximately 7–12 individuals.

Résumé : Des techniques moléculaires nous ont servi à identifier la population d'origine des grand brochets (*Esox lucius*) introduits illégalement dans le lac Davis, Californie, et à étudier la dynamique des changements génétiques depuis cette introduction. Nous avons caractérisé 10 locus microsatellites à quatre nucléotides dans 11 populations et avons utilisé des mesures de différentiation des populations, une analyse phylogénétique et des tests d'assignation pour déterminer l'origine des populations avant et après le traitement à la roténone. Les niveaux de différentiation génétique entre les échantillons du lac Davis avant et après le traitement sont faibles; l'analyse phylogénétique leur attribue tous une forte parenté. Les tests d'assignation placent un fort pourcentage des individus capturés après le traitement dans la population originale du lac Davis. Nos résultats indiquent donc que la population de poissons qui est réapparue en 1999 et les poissons d'un échantillon subséquent en 2002 sont des descendants ou des survivants de la population initiale. Nous sommes incapables d'assigner de façon constante les individus capturés avant ou après le traitement à l'une de plusieurs populations potentielles d'origine, ce qui laisse croire que la source ultime de la population du lac Davis n'a pas été échantillonnée. Il y a des indications dans les échantillons du lac Davis de signatures génétiques d'un goulot d'étranglement récent dans la population; la taille effective de la population durant la période d'échantillonnage était d'environ 7–12 individus.

[Traduit par la Rédaction]

Introduction

The introduction of nonnative species is an increasing threat to the integrity of native ecosystems (Vitousek et al. 1997). Introduced species cause numerous ecological problems, including the extirpation of native species through competition (Bohn and Amundsen 2001), predation (Ogutu-Ohwayu 1993), introduction of novel pathogens (Scott et al. 2001), hybridization with native species (Perry et al. 2002), and alterations of trophic structure (Roemer et al. 2001). All of these processes can have ecosystem-wide effects (Vander Zanden et al. 1999; Townsend 2003). Molecular genetic techniques have proven to be a valuable tool in answering questions relevant to introduced species, including the source of introduced individuals (Jousson et al. 1998; Tsutsui et al. 2001) and changes in effective population size (Planes and Lecaillon 1998).

Northern pike (*Esox lucius*) have been illegally introduced into two lakes in northern California. Pike were discovered in Frenchman Lake in 1988 and were eradicated in 1991 by

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A. Aguilar[1,2] **and R.K. Wayne.** Department of Ecology and Evolutionary Biology, University of California at Los Angeles, 621 Charles E. Young Drive South, Los Angeles, CA 90095, USA.
J.D. Banks and K.F. Levine.[3] State of California, Department of Fish and Game Enforcement Branch, Wildlife Forensics Laboratory, 1701 Nimbus Road, Rancho Cordova, CA 95670, USA.

[1]Corresponding author (e-mail: andres.aguilar@noaa.gov).
[2]Present address: Institute of Marine Sciences and Department of Ocean Sciences, 110 Shaffer Road, University of California, Santa Cruz, CA 95064, USA.
[3]Deceased.

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rotenone, a fish poison to which northern pike are highly susceptible (B. Finlayson, California Department of Fish and Game (CDFG), Pesticides Investigation Unit Suite F, 1701 Nimbus Road, Rancho Cordova, CA 95670, USA, personal communication). Northern pike were found in 1994 in Lake Davis, which is located approximately 20 mi west of Frenchman Lake (CDFG 2003). The discovery of pike in Lake Davis was an immediate concern because the predatory pike posed a threat to the established recreational fishery of Lake Davis. Additionally, the Lake Davis pike population is a serious potential ecological threat to other native fisheries in California because Lake Davis empties into the Sacramento – San Joaquin delta watershed system. This system is home to numerous potential pike prey species, including threatened and endangered species such as Chinook salmon (*Oncorhynchus tshawytscha*) and the Sacramento splittail (*Pogonichthys macrolepidotus*). In 1997, the CDFG performed an extensive rotenone treatment of Lake Davis in an attempt to rid the lake of pike. Northern pike were not definitively documented in Lake Davis until the early summer of 1999, when pike were again discovered by CDFG personnel (CDFG 2003). The return of the pike raised several questions. Were post-rotenone-treatment pike in Lake Davis survivors or descendants of survivors of the pre-rotenone-treatment population or had they once again been illegally reintroduced from another source? If they were survivors, does the decline in effective population size as estimated by molecular genetic techniques provide a measure of the effectiveness of the rotenone treatment? Answers to these questions have important implications for future rotenone treatment and the public role in reestablishing pike. And lastly, can the original source population of Lake Davis pike be identified?

Northern pike are found throughout much of temperate North America and Eurasia. Early studies of northern pike discovered little genetic variation in allozymes for this species throughout its North American range (Seeb et al. 1987). More recent studies using microsatellite loci have found greater levels of genetic variation (Miller and Kapuscinski 1996, 1997; Senanan and Kapuscinski 2000). Northern pike samples from Finland, Siberia, and North America were genetically differentiated (Senanan and Kapuscinski 2000); however, within North America, population affinities were not consistent. The lack of genetic differentiation among North American northern pike populations has been attributed to a number of factors including small effective population sizes (Miller and Kapuscinski 1997) and recent divergence since the last glaciation about 18 000 years ago (Seeb et al. 1987). Homogenization of populations owing to widespread stocking and introduction of fish throughout North America may also be occurring, as this introduces gene flow among populations (Seeb et al. 1987; Miller and Kapuscinski 1997).

To determine the relationships of pre- and post-treatment populations and the population of origin for Lake Davis northern pike, we used phylogenetic techniques and assignment tests. Phylogenetic analysis can prove useful in establishing the relationships of introduced populations. Tsutsui et al. (2001) used phylogenetic analysis of mitochondrial DNA sequences to establish the population of origin for introduced Argentine ants in California and a similar analysis located the origin for a highly invasive algae species in the Mediterranean (*Caulerpa taxifolia*) (Jousson et al. 1998). Assignment tests have been used in empirical studies to address questions of dispersal (Farvre et al. 1997), population structure (Paetkau et al. 1995), introductions (Maudet et al. 2002), and poaching events (Primmer et al. 2000).

To assess the demographic changes associated with rotenone treatment and the treatment effectiveness, we tested for genetic signatures of a population bottleneck. Recent population bottlenecks leave distinct signatures, including heterozygosity excess and allele frequency distortions (Cornuet and Luikart 1996; Luikart and Cornuet 1998; Luikart et al. 1998). These phenomena are somewhat ephemeral in nature, only lasting 0.2–4 N_{e-b} generations (where N_{e-b} is the effective population size of the bottleneck) (Cornuet and Luikart 1996). Nonetheless, statistical signatures have identified population bottlenecks in a number of studies (Luikart et al. 1998), including known introductions of Alpine ibex (*Capra ibex*) (Maudet et al. 2002) and elk (*Cervus elaphus*) (Lenney et al. 2002).

We used the temporal method, developed by Waples (1989), to assess changes in N_e (effective population size) for the Lake Davis northern pike population. The temporal method, which is based on the variance of allele frequencies over time, has been used to monitor effective population size in natural populations (Heath et al. 2002; Waples 2002) and to estimate the effective size of a population bottleneck (Luikart et al. 1999). Evaluation of N_{e-b} (Luikart et al. 1999; Spencer et al. 2000) is important not only from a conservation perspective (Funk et al. 1999; Heath et al. 2002) but also to determine the effectiveness of population control measures. The temporal method has also been used to evaluate the ratio of N_e to census population size (N), a value that can be much less than 1 in some populations (Hauser et al. 2002; Turner et al. 2002) and that provides an important perspective on breeding dynamics, life history traits, and other factors that can cause departures of effective population size from the census size.

In summary, we utilized phylogenetic analysis and assignment tests to determine the origin of pre- and post-rotenone-treatment northern pike in Lake Davis, California. Lake Davis individuals were compared with 11 putative source populations. We also used bottleneck tests to assess the genetic effect and effectiveness of rotenone treatment on the population. Lastly, we used two distinct methods (Waples 1989; Berthier et al. 2002) to empirically estimate the effective size of the Lake Davis population through time.

Methods

Samples

We sampled 67 pretreatment fish from 1997 (Lake Davis-97), 76 posttreatment fish from 1999 (Lake Davis-99), and 46 posttreatment fish from 2002 (Lake Davis-02). We also sampled populations of native and introduced northern pike populations in western North America (Table 1). We sampled the following seven lake populations in Idaho: Anderson, Benewah, Blue, Cave, Chatcolet, Killarney, and Medicine lakes. The samples from Palmer, Alaska, are from

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Table 1. Populations used in this study, codes, and samples sizes.

Source	Code	Sample size
Western North America		
Palmer, Alaska	AKA	10
Long Lake, Arizona	AZL	48
Parker Canyon Lake, Arizona	AZP	30
Wellington, Colorado	COL	9
Idaho lakes	IDA	31
Basset Lake, Nevada	NEV	9
Native Range North America		
Isle Royal, Michigan	IRM	10
Moose River, Minnesota	MRM	9
St. Lawrence River, New York	NY	40
Tom Cod, Minnesota	TCM	10
Red Lake, Wisconsin	WIS	13

an introduced population that likely derived from a native Alaskan source. Our sampling has not included many populations from the "native" range of North American northern pike. We have concentrated on introduced pike populations in the western part of the continent because Lake Davis northern pike were most likely transported over land from a close source. Unfortunately, for this study, samples from the population that existed at Frenchman Lake were not available. Over the eradication period, the majority of fish removed were young of the year, with 93% of the individuals measuring less than 270 mm (CDFG 2003). Twenty-eight (42%), 71 (93%), and 46 (100%) of the individuals genotyped were classified as yearlings (based on this size criterion) for the 1997, 1999, and 2002 samples, respectively.

Muscle, gill raker, fin clip, or scales were used as a source for DNA extraction. DNA was extracted using one of two protocols. Tissue was digested either in CTAB extraction buffer followed by phenol–chloroform extraction (muscle) or by using a QIAGEN DNA extraction kit (QIAGEN Inc., Valencia, Calif.) (all other tissues). For the CTAB extraction, 0.5 g of tissue was minced and placed into 600 µL of 2× CTAB extraction buffer (Saghai-Maroof et al. 1984) with 0.5 mg of proteinase-K. The sample was then shaken at 55 °C for 4–12 h until completely digested. The crude extract was then subjected to two extractions (equal volumes) in phenol – chloroform – isoamyl alcohol (25:24:1) and one extraction (equal volume) in chloroform – isoamyl alcohol (24:1). DNA was then precipitated in an equal volume of isopropanol at –20 °C and resuspended in Tris–EDTA buffer. The manufacturer's protocol was followed for the QIAGEN extraction kit.

Microsatellite markers

We used 11 tetranucleotide repeat loci developed for northern pike by Genetic Identification Services (Northridge, California). Microsatellite allele sizes were scored using the Beckman-Coulter CEQ2000 capillary system (Beckman-Coulter Inc., Fullerton, California). One primer in each direction was labeled with one of three commercially available dyes (Invitrogen Corporation, Carlsbad, California) (Table 2). Each locus primer was designed so that products could be amplified under the same polymerase chain reaction conditions. We used 10-µL reaction volumes to which 20–50 ng of genomic DNA, 0.2 µmol each primer·L^{-1}, 1.0 mmol $MgCl_2$·L^{-1}, 50 µmol dNTPs·L^{-1}, 1× Sigma polymerase chain reaction buffer (10 mmol Tris–HCl·L^{-1} (pH 8.0) and 50 mmol KCl·L^{-1}), and 2.5 units of Taq polymerase were added. Loci were pooled so that three to five loci were run per lane. Allele size scoring was done with the Beckman-Coulter gene analysis system software.

Table 2. List of the tetranucleotide microsatellite loci of northern pike (*Esox lucius*) and forward and reverse primers used in this study.

Locus	Primer	Sequence (5′–3′)
B 16	Forward	TGG GGA GAG GGA AGT CTG[a]
	Reverse	GCA ATG GAC CAA AAA AGG A
B 24	Forward	TGA AAT TCA CTT GTT GTG TCT G
	Reverse	GTC CGC TGT TGA CCT TTT
B 25	Forward	GTC ACC GTG GTC TGT CAG[a]
	Reverse	TGG GTA ATG GAG AGA AAG AA
B 117	Forward	TGA CCG ACA TAC CGT AAC TC[a]
	Reverse	GGA TGA AGT GAT AAG GAT GGT
B 246	Forward	AAC CCA TCA AAG ACA TCA GC
	Reverse	GCC AGA GAC AAC ATA GCG A[a]
B 259	Forward	AGG CTC CAC TGT AAA TGC TTT[a]
	Reverse	GTG CTA AAG GGA GGA CTT CTG
B 281	Forward	GGA AAT TCC TCC ATT TTG TTT G
	Reverse	GCA TCC CAT CTT TTT GGA AA[a]
B 304	Forward	CCT TCA GAT CAG TAA TGT CAG C
	Reverse	AGG TCA GTG AGG ACA GAG GT[a]
B 422	Forward	TGA CTG TGT GAG TCT GTA AGA
	Reverse	ACA ACT GGC CTT GAG AG[a]
B 451	Forward	CTG GAT CAC TGT CTC TTT TCT G
	Reverse	GAG AGG GTG AGA ACA CCA GT[a]
B 457	Forward	CTG TCC ACC TCT TGG TCT[a]
	Reverse	AGG GAG TGT TAG AGA TGG AT

[a]Dye-labeled primer.

Data analysis

Basic population genetic statistics for microsatellites were calculated using GENEPOP (Raymond and Rousset 1995). Populations were tested for deviations from Hardy–Weinberg equilibrium at each locus (Guo and Thompson 1992) as well as for gametic disequilibrium in GENEPOP (Garnier-Gere and Dillmann 1992). Bonferroni corrections were made for multiple comparisons. Population differentiation, measured as pairwise F_{ST} (θ) (Weir and Cockerham 1984), was estimated for all population pairs using the program GENETIX (Belkhir 1999). Significance for these estimates was established using a bootstrap procedure with 500 replicates. The Idaho populations were pooled into one population, as they were not significantly differentiated from each other (F_{ST} = 0.04, 95% confidence interval (CI) = –0.02 to 0.09, CI based on 1000 bootstrap replicates (Weir and Cockerham 1984)). Pooling of these populations did not lead to a value of F_{IS} significantly different from zero or significant linkage disequilibrium (after correction for comparison of eight variable loci). The two populations from Minnesota (Moose River and Tom Cod) were also pooled for the dis-

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tance and assignment analyses owing to low F_{ST} values (F_{ST} = –0.004, 95% CI = –0.02211 to 0.01523), and this pooling also did not lead to any significant changes in Hardy–Weinberg (F_{IS}) or linkage equilibrium (after correction for 10 pairwise comparisons).

We applied two tests to the microsatellite data to determine the origin of the Lake Davis samples: (*i*) a fully Bayesian-based clustering method (Pritchard et al. 2000) and (*ii*) a frequency-based approach (Paetkau et al. 1995). For both methods, the Lake Davis-99 and Lake Davis-02 individuals were designated as having a population of unknown origin and assigned to a panel of sampled reference populations (Lake Davis-97, Nevada, Idaho, etc.). We also conducted the same tests to assign individuals from the pretreatment population (Lake Davis-97) to the reference panel (i.e., all populations except pre- and post-treatment Lake Davis pike). For the fully Bayesian clustering method, STRUCTURE (Pritchard et al. 2000) was used to classify individuals according to a Bayesian framework. Prior population information was used for the reference populations, and the number of populations (K) was set to 7. A burnin period of 100 000 steps was followed by 250 000 iterations. Here, the no admixture model was assumed and individuals were assigned to a population if the probability of assignment (T) was greater than 0.95. The frequency-based test was performed with the program WHICHRUN (Banks and Eichert 2000), which uses the frequency-based assignment approach of Paetkau et al. (1995). The "critical" population test was used to assign the posttreatment individuals, with the pretreatment population used as the critical population. This method compares the ratio of the assignment probability to the critical population (Lake Davis-97) with that of the next most likely population. The $\log_{10}$ of the ratio gives a measure of the relative strength of assignment to the most likely population. The critical population log of odds score was set at 2 and therefore the chance of error at 0.01 or less (Banks and Eichert 2000).

We analyzed the microsatellite data using clustering techniques to assess the topological relationship of populations. UPGMA (unweighted pair group method using arithmetic averages) trees were constructed with the program POPULATIONS (Langella 2002) using the distance measures $\delta\mu^2$ (Goldstein et al. 1995) and D_{AS} (Jin and Chakraborty 1993). Five hundred bootstrap replicates were done for each population tree to assess support of population groupings.

To test for genetic homogeneity of the Lake Davis samples over time, we used STRUCTURE to determine the number of distinct populations (K) inhabiting the lake during our sampling period (Lake Davis-97 through Lake Davis-02). An admixture model was assumed, and the probability of the data was estimated for K = 1–5. A burnin period of 100 000 steps was followed by 250 000 iterations. Posterior probabilities for each estimate of K were estimated using the log-likelihood values for each K.

To evaluate changes in N_e, we analyzed the Lake Davis-97, Lake Davis-99, and Lake Davis-02 samples for the genetic signature of a population bottleneck. We tested for allele frequency distortions and heterozygosity excess using the BOTTLENECK computer program (Piry et al. 1999). Population bottlenecks lead to a mode shift in allele frequency distributions, as a population that has undergone a recent bottleneck contains fewer rare alleles (shifted mode) than a population that is at mutation-drift equilibrium (a nonbottlenecked population has an L-shaped distribution) (Luikart et al. 1998). The loss of rare alleles also causes a heterozygosity excess in a population that has undergone a recent bottleneck (Hedrick et al. 1986); thus, a second test compares expected Hardy–Weinberg heterozygosity (H_e) with the expected heterozygosity for an equilibrium population (H_{eq}) (Cornuet and Luikart 1996). The H_{eq} is estimated using the number of alleles and sample size from a population. We used only the Wilcoxon signed-ranks test (Piry et al. 1999) to evaluate heterozygosity excess, as this test has more power than the sign test and takes into account the degree of heterozygosity excess in a population (Luikart and Cornuet 1998; Piry et al. 1999). The standardized differences test could not be used because it requires more than 10 microsatellite loci (see Results) (Cornuet and Luikart 1996). The two-phase model was used to calculate H_{eq}, with 1000 iterations and 95% single-step mutations (12% variance of multistep mutations) as suggested by Piry et al. (1999).

To evaluate changes in N_e, we followed the approach of Waples (1989), which is based on temporal changes in allele frequencies, and that of Berthier et al. (2002), which is a likelihood-based estimator of N_e. Because the generation time in pike is approximately 4 years (Miller and Kapuscinski 1997), we could only assess changes in N_e for the Lake Davis population between the initial (1997) and final sampling periods (2002). Individuals sampled in 2002 were all young of the year (based on size), and we therefore assume that they are at a minimum one generation separated from the 1997 young of the year individuals. To obtain a range of N_e estimates, we used the plan I and II estimators (Waples 1989). A conservative estimate of population census size of 500 individuals was used, as the number of individuals captured generally exceeds this value (CDFG 2003). The harmonic mean of samples sizes (S) was calculated between sampling periods (0 and t (t = number of generations between sampling events)) (Waples 1989). Per-locus variance in allele frequencies (F_k) was calculated using the approach of Pollak (1983). Confidence intervals for F_k were calculated following Waples (1989). The program tm3.1 (http://www.rubic.rdg.ac.uk/~mab/software.html) was used to estimate N_e for the likelihood-based method. The maximum population size was set to 500, and a total of 100 000 iterations were run. The analysis was preformed multiple times to ensure convergence of the Markov chain.

As an alternative method to estimate the number of breeders in Lake Davis through our sampling period, we used the approach outlined in Emery et al. (2001). This method was used to estimate the combined number of mothers and fathers consistent with the young of the year that were sampled in 1997, 1999, and 2002 with the computer program PARENTAGE (www.maths.abdn.ac.uk/~ijw). This method is a Bayesian approach and requires no information about potential parental genotypes (Emery et al. 2001). A burnin period of 50 000 steps was used prior to sampling, with 5000 samples taken every 400 iterations following the initial burnin period. Prior distributions were set for mutation rate (gamma distribution with shape parameter of 2 and mean

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0.001) and α and β (distribution of offspring for males and females, respectively). The α and β parameters had a gamma distribution with shape parameter of 1 and a mean of 0.25. Varying the α and β parameters did not change the overall number of parents for each of the sampling periods. Posterior distributions were then evaluated for the overall number of parents.

Results

A total of 11 tetranucleotide repeats were initially typed in 408 northern pike. Of these 11 loci, 10 could be scored confidently and were used in the analysis (Table 2). None of the microsatellite loci deviated significantly from Hardy–Weinberg equilibrium, nor was any gametic disequilibrium apparent between loci within populations after sequential Bonferroni corrections. The New York population exhibited the greatest amount of variation, with a mean of 7.6 alleles per locus and a mean heterozygosity of 0.68. The Alaska population had the lowest observed heterozygosity of 0.26, and the mean number of alleles was 1.9. Genetic variability was high for the Lake Davis populations when compared with other introduced pike populations (Table 3). The mean number of alleles for Lake Davis-97, Lake Davis-99, and Lake Davis-02 was 4.2, 4.2, and 3.9, whereas the mean number of alleles for the Alaska, Arizona – Long Lake, Arizona–Parker, Colorado, Idaho, and Nevada populations was 1.9, 3.6, 2.6, 3.3, 2.7, and 4.1, respectively.

Origin of posttreatment northern pike

Values of pairwise population differentiation (F_{st}) varied greatly between populations (Table 4). Overall F_{st} among all populations was 0.198 (95% CI = 0.168–0.230). Pairwise values of F_{st} between the Lake Davis populations and all other populations were small but significantly different from zero (Table 4). For Lake Davis populations, the greatest amount of differentiation was observed between the Lake Davis-97 and Lake Davis-02 samples (F_{st} = 0.029). However, the three Lake Davis populations showed less differentiation between each other than they did with other populations (Table 4).

Likewise, genetic distance trees showed that all of the Lake Davis samples are more closely related to one another than to any of the other populations sampled for both the D_{AS} and $\delta\mu^2$ distance measures. The Lake Davis samples define a distinct cluster supported by moderate bootstrap values (Fig. 1). However, a close relationship of the Lake Davis population to any of the putative source populations was not obvious. Other groupings that were supported by moderate bootstrap values were the Colorado and Arizona – Long Lake populations (both trees) and a grouping that contained the Wisconsin, New York, and Minnesota populations (Fig. 1*a*). Alaska was the most divergent population.

The frequency-based assignment method classified 75 of 76 posttreatment Lake Davis-99 individuals to the pretreatment population (Table 5). One individual was assigned to the Nevada population, with the second most probable population of origin being Minnesota. Sixty-six of the Lake Davis–99 posttreatment individuals were assigned to the pretreatment population (designated critical population) with a log of odds score of 2 or greater. This method also assigned 44 of 46 Lake Davis-02 samples to the pretreatment sample, 36 of these passing the critical population criterion (Table 5). The two remaining individuals were assigned to the Colorado population and the Minnesota population. The second most likely population of assignment for these individuals was Nevada and Lake Davis, respectively.

Most individuals from the Lake Davis-99 and Lake Davis-02 samples had the highest probability of belonging to the pretreatment population using STRUCTURE, although the stated criterion was not met in some cases. STRUCTURE assigned 75 of 76 Lake Davis-99 individuals and 45 of 46 Lake Davis-02 individuals to the Lake Davis-97 population ($T > 0.95$) (Table 5). The same individual from the Lake Davis-99 sample (P2051) that was assigned to the Nevada population in the frequency-based test was also assigned with high probability to the Nevada population using STRUCTURE, although the assignment probability was not above our established criterion ($T > 0.95$). One individual from the Lake Davis-02 sample was assigned to the Minnesota population with the frequency test but was assigned to the Lake Davis-97 population with STRUCTURE. However, the assignment probability did not exceed the $T = 0.95$ criterion.

The results from STRUCTURE indicate that the individuals sampled over our entire sampling period from Lake Davis form a single genetic unit. When K was set to equal 1, the likelihood of the data was the highest (–4380.6). All other likelihood estimates decreased when K increased. The posterior probability for $K = 1$ was approximately 1, while posterior probabilities for all other K values (2–5) were less than 0.0001.

The total number of northern pike removed by CDFG personnel increased dramatically from 1999 (197 individuals) to over 10 000 individuals in 2002 (CDFG 2003). Our 2002 samples consisted solely of young of the year individuals, which is the dominant age-class in the total sample (93%; CDFG 2003) and suggests that northern pike are reproducing within Lake Davis. This observation, coupled with the fact that individuals older than 3 years of age are found during removal efforts (CDFG 2003), provides an independent line of evidence that pike have survived and flourished after the rotenone treatment in 1997.

Origin of pretreatment northern pike

As in the phylogenetic analysis, individuals belonging to the pretreatment (Lake Davis-97) sample were not assigned consistently to a single source population (Table 5). With the frequency-based approach, a majority of individuals were assigned to two populations. Twenty-two individuals were assigned to the Minnesota population and 22 were assigned to the Colorado population. These data, when analyzed with STRUCTURE, were unable to consistently assign the Lake Davis-97 individuals to any one source population with the stated assignment threshold.

Changes in effective population size

Pre- and post-treatment Lake Davis samples showed evidence of a recent population bottleneck. Wilcoxon's test for heterozygosity excess was significant for all Lake Davis

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Table 3. Sample sizes (N), number of observed alleles (k), and observed (H_o) and expected (H_e) heterozygosity for the 10 microsatellite loci used in this study.

Locus	LD-97	LD-99	LD-02	AKA	AZL	AZP	COL	IDA	NEV	IRM	MRM	NY	TCM	WIS
304														
N	67	76	46	9	29	29	8	38	9	10	8	37	9	13
k	4	4	4	1	2	2	3	1	3	2	3	4	3	4
H_o	0.687	0.776	0.652	—	0.172	0.517	0.750	—	0.222	0.500	0.500	0.405	0.444	0.385
H_e	0.712	0.721	0.724	—	0.216	0.487	0.608	—	0.216	0.394	0.433	0.437	0.386	0.612
246														
N	65	71	45	9	29	28	8	36	9	9	9	37	7	11
k	4	3	3	2	3	2	3	3	3	3	3	5	4	3
H_o	0.538	0.507	0.333	0.333	0.621	0.143	0.250	0.250	0.778	0.556	0.222	0.757	0.429	0.455
H_e	0.530	0.501	0.400	0.503	0.557	0.135	0.633	0.227	0.660	0.621	0.464	0.673	0.396	0.542
422														
N	66	76	45	9	29	29	8	38	9	10	9	37	10	13
k	5	6	5	2	5	2	4	1	5	5	4	7	5	5
H_o	0.788	0.789	0.689	0.667	0.655	0.448	0.750	—	0.778	0.400	0.889	0.865	0.600	0.308
H_e	0.781	0.793	0.723	0.471	0.740	0.354	0.725	—	0.680	0.726	0.673	0.799	0.737	0.582
117														
N	61	68	46	9	29	29	6	38	9	10	9	38	10	12
k	3	3	2	1	2	2	2	3	3	4	4	6	5	4
H_o	0.475	0.412	0.522	—	0.483	0.552	0.833	0.263	0.556	0.700	0.667	0.605	0.500	0.583
H_e	0.475	0.429	0.410	—	0.494	0.503	0.530	0.235	0.464	0.574	0.575	0.659	0.695	0.659
259														
N	66	76	46	9	29	29	8	38	9	10	9	38	8	13
k	6	4	4	4	3	3	2	3	4	3	5	8	3	3
H_o	0.712	0.724	0.696	0.444	0.586	0.724	0.625	0.526	0.556	0.500	0.667	0.658	0.750	0.308
H_e	0.751	0.725	0.702	0.673	0.465	0.624	0.525	0.563	0.699	0.511	0.739	0.641	0.642	0.342
281b														
N	66	76	46	9	29	28	8	38	8	10	9	38	10	13
k	2	3	2	1	4	3	3	2	5	3	2	5	2	3
H_o	0.364	0.447	0.500	—	0.586	0.607	0.500	0.105	0.750	0.800	0.222	0.395	0.200	0.308
H_e	0.370	0.492	0.477	—	0.533	0.491	0.425	0.147	0.767	0.584	0.366	0.395	0.189	0.342
24														
N	66	76	46	9	29	29	8	38	9	10	9	38	10	13
k	6	5	6	2	3	4	5	5	3	5	6	11	7	6
H_o	0.818	0.789	0.652	0.111	0.552	0.759	0.875	0.474	0.667	0.700	0.778	0.947	0.700	0.769
H_e	0.739	0.749	0.745	0.425	0.511	0.619	0.758	0.626	0.686	0.811	0.830	0.895	0.863	0.849
457														
N	67	75	45	9	29	28	7	37	9	8	6	38	9	11
k	4	4	4	1	4	2	3	3	5	3	4	7	5	7
H_o	0.582	0.627	0.733	—	0.655	0.571	0.571	0.541	0.778	0.500	0.833	0.605	0.778	0.909
H_e	0.635	0.662	0.608	—	0.694	0.468	0.648	0.431	0.680	0.633	0.712	0.659	0.693	0.823
451														
N	67	76	46	9	28	27	7	37	9	9	9	38	10	13
k	5	6	5	3	5	4	3	4	6	7	9	14	10	9
H_o	0.716	0.724	0.652	0.556	0.379	0.519	0.571	0.541	0.778	0.889	0.778	0.789	0.700	0.615
H_e	0.756	0.688	0.616	0.523	0.547	0.505	0.641	0.634	0.732	0.869	0.869	0.915	0.937	0.877
16														
N	67	71	46	9	29	29	8	38	9	10	9	38	9	13
k	4	4	4	2	5	2	5	2	4	4	5	9	5	5
H_o	0.642	0.648	0.652	0.444	0.862	0.414	1.000	0.026	0.778	0.600	0.556	0.737	0.444	0.846
H_e	0.609	0.597	0.578	0.366	0.750	0.479	0.808	0.026	0.575	0.557	0.804	0.762	0.712	0.770
Mean														
k	4.2	4.2	3.9	1.9	3.6	2.6	3.3	2.7	4.1	3.9	4.5	7.6	4.9	3.3
H_o	0.634	0.644	0.608	0.256	0.557	0.525	0.673	0.273	0.664	0.614	0.611	0.676	0.555	0.673
H_e	0.6377	0.636	0.598	0.296	0.553	0.467	0.635	0.289	0.616	0.628	0.647	0.683	0.625	0.635

Note: LD indicates Lake Davis samples. See Table 1 for other population codes.

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Table 4. Pairwise F_{ST} (above diagonal) and genetic distances (below diagonal) between the sampled populations.

	LD-97	LD-99	LD-02	AKA	AZL	AZP	COL	IDA	NEV	IRM	MIN	NY	WIS
LD-97	—	**0.006**	**0.029**	0.364	0.220	0.254	0.171	0.324	0.200	0.162	0.113	0.120	0.165
LD-99	**0.011/0.028**	—	**0.018**	0.356	0.230	0.260	0.187	0.337	0.190	0.169	0.122	0.125	0.178
LD-02	**0.061/0.157**	**0.034/0.224**	—	0.360	0.253	0.287	0.207	0.375	0.219	0.167	0.132	0.133	0.212
AKA	0.68/36.222	0.66/46.112	0.65/36.216	—	0.435	0.439	0.436	0.628	0.412	0.417	0.362	0.307	0.362
AZL	0.42/2.042	0.44/2.056	0.45/2.17	0.66/4.776	—	0.259	0.056	0.370	0.197	0.141	0.126	0.101	0.168
AZP	0.45/1.317	0.47/1.361	0.48/1.338	0.56/2.821	0.36/1.424	—	0.212	0.462	0.297	0.282	0.178	0.173	0.218
COL	0.37/1.989	0.41/2.06	0.41/2.139	0.63/4.902	0.10/0.254	0.28/1.009	—	0.377	0.190	0.148	0.080	0.073	0.127
IDA	0.48/1.251	0.52/1.279	0.51/1.042	0.69/5.485	0.42/4.234	0.53/1.478	0.42/4.026	—	0.440	0.366	0.226	0.263	0.323
NEV	0.41/2.09	0.39/1.891	0.42/2.617	0.58/3.312	0.32/3.133	0.46/0.271	0.37/2.965	0.49/2.122	—	0.144	0.142	0.122	0.178
IRM	0.36/4.289	0.37/4.114	0.32/4.131	0.65/8.405	0.21/5.62	0.42/2.688	0.30/5.872	0.39/0.87	0.27/0.934	—	0.060	0.078	0.147
MIN	0.23/2.472	0.25/0.442	0.25/0.322	0.57/8.848	0.22/0.832	0.36/0.890	0.16/1.971	0.24/0.704	0.30/0.775	0.14/92.595	—	−0.005[a]	0.059
NY	0.26/0.534	0.26/0.46	0.27/0.445	0.53/6.353	0.18/92.127	0.30/1.429	0.17/4.167	0.35/7.267	0.26/2.337	0.19/24.008	0.03/60.251	—	0.041
WIS	0.35/91.314	0.38/61.228	0.42/91.107	0.55/24.667	0.29/2.60	0.31/60.941	0.25/2.529	0.32/70.758	0.35/2.169	0.31/62.514	0.11/40.475	0.08/30.672	—

Note: Pairwise comparisons between Lake Davis (LD) samples are in bold. D_{AS} distances are above the $\delta\mu^2$ distances. See Table 1 for site codes.
[a]Nonsignificant value ($p > 0.05$).

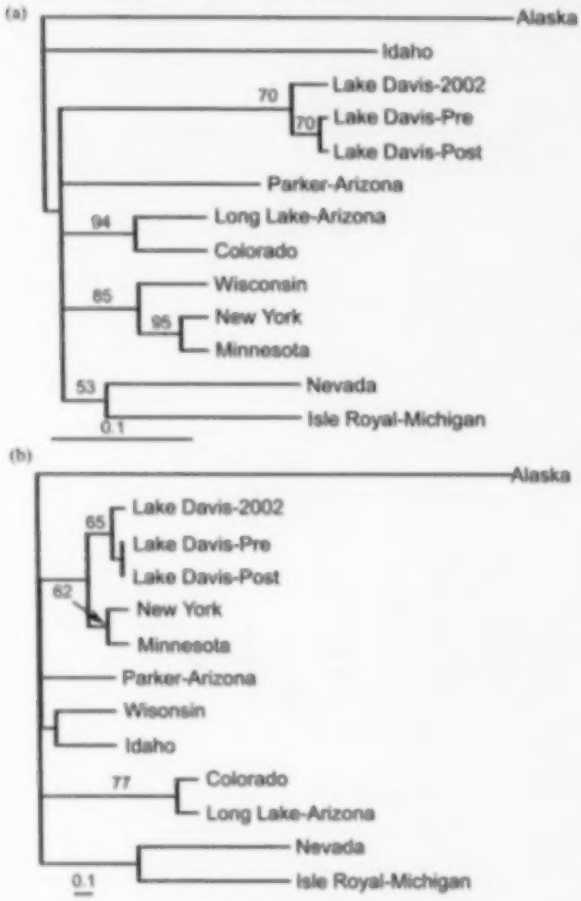

Fig. 1. UPGMA (unweighted pair group method using arithmetic averages) trees based on the (*a*) D_{AS} (allele sharing distance) and (*b*) $\delta\mu^2$ distance measures. Bootstrap values above 50% are shown on the trees. Scale in genetic distance units is shown.

sampling periods (Lake Davis-97: $p = 0.0005$; Lake Davis-99: $p = 0.002$; Lake Davis-02: $p = 0.009$). Allele frequency distribution distortions were evident for the Lake Davis-97 and Lake Davis-99 samples with a decrease in the proportion of rare alleles (shifted mode) but not the Lake Davis-02 sample (L-shaped distribution) (Fig. 2).

The temporal estimate of effective population size from the 1997–2002 sampling period was 12 (95% CI = 7–71) for the plan I estimate and 11 (95% CI = 8–55) for the plan II estimate. The estimate of allele frequency change (F_k) was 0.071 (95% CI = 0.022–0.092). The likelihood-based estimator of N_e between the 1997 and 2002 sampling periods was 7 (95% CI = 5–15). Although there has not been a population size census for Lake Davis, yearly capture numbers are markedly higher than the estimate of N_e (2002: >10 000 individuals; CDFG 2003).

Analysis from the PARENTAGE program yielded different numbers of parents contributing to the young of the year samples from 1997, 1999, and 2002. From 12 to 16 parents

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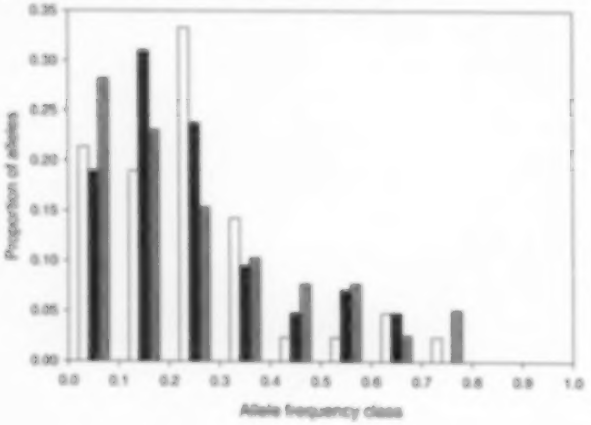
Table 5. Results of the assignment test for the pre- (LD-97) and post-treatment (LD-99 and LD-02) Lake Davis individuals.

			Source						
Method	Population	*N*	LD-97	COL	NEV	IRM	MIN	NY	WIS
Frequency	LD-99	76	75/66[a]		1/–				
	LD-02	46	44/36[a]	1/–			1/–		
STRUCTURE	LD-99	76	75						
	LD-02	46	45						
Frequency	LD-97	67		22	7	9	22	1	6

Note: For the STRUCTURE analysis, only individuals with assignment probabilities (T) greater than 0.95 are indicated. See Table 1 for site codes.
[a]The second number indicates the number of individuals passing the log of odds test.

Fig. 2. Allele frequency distortion graph for the three Lake Davis northern pike (*Esox lucius*) samples. Open bars, solid bars, and shaded bars indicate the Lake Davis pretreatment, posttreatment, and 2002 samples, respectively.



gave rise to the yearling sample from 1997, 22–27 parents were found for the 1999 sample, and 14–19 parents were found for the 2002 yearlings (all with a posterior probability of >95%). The most probable number of parents for the 1997, 1999, and 2002 yearling samples was 14 (31.9% posterior probability), 24 (31% posterior probability), and 16 (30.5% posterior probability), respectively. The harmonic mean of breeders over this time period is 17.

Discussion

Origin of posttreatment northern pike

Our data indicate that the posttreatment Lake Davis fish (Lake Davis-99 and Lake Davis-02) are survivors and (or) descendants of the population that inhabited the lake prior to rotenone treatment in 1997. There are three lines of evidence that support this conclusion: (*i*) low differentiation between the three Lake Davis populations as compared with other populations, (*ii*) high assignment probabilities of posttreatment individuals to the pretreatment population with the two assignment tests that we utilized, and (*iii*) the annual production of young of the year individuals following the rotenone treatment.

The Lake Davis population has not changed appreciably in levels of genetic differentiation over time. Low effective population sizes and population bottlenecks can affect the temporal component of genetic differentiation within a population by causing a change in allele frequencies (Wright 1969; Maruyama and Fuerst 1985). Similarly, reintroduction of the Lake Davis population after the rotenone treatment in 1997 with individuals that were genetically different from the initial source would lead to a higher degree of population differentiation than that which we observed. However, we observed no increase in the temporal aspect of population differentiation across sampling periods. This result suggests that a substantial number of individuals survived the rotenone treatment and excludes the possibility of a large-scale reintroduction from another source population. The presence of young of the year fish in 1999 and 2002 suggests in situ reproduction for the Lake Davis pike population, further supporting the notion that older fish had survived the initial rotenone treatment and were breeding within Lake Davis.

Genetic distance analysis showed a close relationship among the Lake Davis temporal samples for a number of distance measures. As above, this supports the notion that the post-rotenone-treatment individuals found in Lake Davis are survivors of the initial treatment. Similarly, the close relationship between the introduced pike populations from Colorado and Long Lake, Arizona, implies that they may have been introduced from the same source or that one of the populations gave rise to the other. Another recently introduced population, Parker Canyon Reservoir, Arizona, did not show a close affinity to a potential source population in Long Lake, Arizona.

A possible explanation of our results is that a large number of posttreatment fish may have been reintroduced by humans from the same initial source population of Lake Davis pike. The individual(s) who initially placed pike into Lake Davis pre-1994 would conceivably have access to the same stock of fish for reintroduction following the rotenone treatment in 1997. However, this reintroduction would have to be large, on the order of several hundred individuals (see above), to account for the amount of variation that is observed in both of the posttreatment samples. A severe bottleneck, imposed by the reintroduction of a small number of individuals, would manifest itself not only in bottleneck tests but also as a dramatic loss in allelic diversity (Bouzat et al. 1998; Hoelzel 1999) or greater variance in allele frequencies ($\hat{F}_k$) (Waples 1989; Luikart et al. 1999). We did not observe a loss in gene diversity, as there are only three of 41 alleles from three loci that were present in the pretreatment population that are absent in either of the posttreatment samples. Further, the $\hat{F}_k$ estimate for N_e of 12 and the likelihood estimate for N_e of 7 for 1997–2002 imply that a large census population size existed throughout the period (see below).

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Origin of pretreatment northern pike

We were not able to find the ultimate source population for the Lake Davis northern pike, as the assignment tests did not identify any of our putative sources as the population of origin for our pretreatment samples. Genetic distance analysis did not reveal any close relationships between the Lake Davis samples and any other population. The source for the Lake Davis population may be difficult to resolve owing to the lack of genetic differentiation among populations (Senanan and Kapuscinski 2000), the fact that northern pike have been extensively stocked throughout North America (Page and Burr 1991; McMahon and Bennett 1996), and (or) that we have not sampled the original source population for Lake Davis. The Lake Davis fish could have been introduced from the population that inhabited Frenchman's Flat Reservoir; however, no samples of these fish were collected following the treatment of this reservoir (N. Villa, CDFG, 1701 Nimbus Road, Suite A, Rancho Cordova, CA 95670, USA, personal communication). Alternatively, the Lake Davis population could have been introduced from multiple sources. However, if all putative source populations were sampled, then the assignment methods should be able to consistently assign individuals to these populations, and this was not the case. Also, the mixing of two or more genetically distinct stocks in Lake Davis would lead to extensive linkage disequilibria and deviations from Hardy–Weinberg equilibrium immediately following the introduction (Hartl and Clark 1997). Neither is observed in any of the Lake Davis populations, indicating that Lake Davis is derived from one stock. Results from the STRUCTURE analysis of all Lake Davis individuals indicate that the fish that we sampled are from a single genetic unit, which also supports the notion of a homogeneous population within the lake.

Changes in effective population size

Past population bottlenecks are evidenced in the Lake Davis temporal samples as shown by the Wilcoxon signed-ranks test for heterozygosity excess as well as mode shifts in allele frequency distributions in the Lake Davis-97 and Lake Davis-99 samples. The signature of a bottleneck may stem from the initial introduction of individuals into Lake Davis. The timing for the initial introduction of individuals into Lake Davis is likely close to their time of discovery in 1994, and population bottleneck signatures may persist as long as 4 $N_{e\text{-}b}$ generations (Cornuet and Luikart 1996). The Lake Davis-02 samples, although testing positive for heterozygosity excess, do not show evidence of a population bottleneck from the allele frequency distortion graphs. This finding may indicate that the population is recovering from the initial population introduction or from a bottleneck introduced by the rotenone treatment of Lake Davis in 1997. However, if the population suffered a dramatic decline in numbers, then the signature of a bottleneck should still be evident for both heterozygosity excess tests and the allele frequency distortions in the Lake Davis-02 samples, as these samples are at most separated by one generation or 4 years from the time of treatment.

Estimates of N_e using the temporal and likelihood-based methods indicated a low N_e during the 1997–2002 interval, which may be due to the treatment of the initial population or the current management of the Lake Davis population. As an independent estimator of N_e, the harmonic mean for the number of breeders obtained from the PARENTAGE analysis was 17, which falls within the 95% CI for the temporal estimate of N_e. This indicates that even though treatment of Lake Davis was extensive, a viable population persisted through the treatment event. It should be noted that N_e/N (effective population size/census size) might be as low as 0.03–0.14 in northern pike populations (Miller and Kapuscinski 1997), which implies that a large number of individuals (>600) may have survived the rotenone treatment.

The analytical tools that we have applied to the Lake Davis pike are of general importance to the management of this population and have implications for the control and monitoring of other introduced species. Genetic information on introduced populations can provide insight into the origin of introduced populations (Hauser et al. 1998) and, as we show, can provide an assessment of the effectiveness of an eradication program. In cases for which eradication is not possible, the molecular genetic techniques that we have applied can be used to assess containment efficacy and to monitor changes in N_e (Waples 1989). For example, our results suggesting low effective population size imply that control efforts are having an effect but are ineffectual in eliminating pike from Lake Davis. In the future, pike may migrate to other parts of the Sacramento River drainage, and our results suggest that Lake Davis can be identified as a putative source. Also, genetic information from the Lake Davis population would prove useful in legal cases for which individuals are suspected of transporting or introducing northern pike into California. Finally, given the serious consequences of northern pike migration into the Sacramento watershed, it would appear advisable for the CDFG to continue genetic monitoring to assess their success in suppressing the breeding population.

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A continuum of life history tactics in a brown trout (*Salmo trutta*) population

Julien Cucherousset, Dominique Ombredane, Katia Charles, Frédéric Marchand, and Jean-Luc Baglinière

Abstract: Life history tactics of the brown trout (*Salmo trutta*) population of the Oir River (Normandy, France) were studied using passive integrated transponder (PIT) tagging data of five consecutive cohorts (5900 individuals) monitored between 1995 and 2002. Results demonstrate that (*i*) life history traits vary among cohorts, chiefly caused by environmental variability, (*ii*) juvenile growth, particularly second-year growth, plays an important role in the determination of the growing environment and trout exhibit variable migratory behaviour (from remaining in the natal brook to migrating in the sea) related to their juvenile growth rate, and (*iii*) the description of life history tactics (including juvenile growth, fine-scale migratory behaviour, and reproduction) can be clarified. Tactics are expressed along a continuum in time (age to reproduce) and space (distance of migration). Flexible life history tactics varying with juvenile growth is consistent with previous studies, but the use of empiric data on growth and migration from PIT tagging allows refining the description of life history tactics, taking into account their continuous distribution in time and space.

Résumé : Les tactiques d'histoire de vie de la population de truite commune (*Salmo trutta*) de l'Oir (Normandie, France) ont été étudiées par le marquage individuel à l'aide de « PIT tag » de cinq cohortes consécutives (5 900 individus) suivies de 1995 à 2002. Les résultats confirment et démontrent que (*i*) les traits d'histoire de vie varient entre les cohortes et que cette variabilité peut être reliée principalement aux fluctuations des conditions environnementales, (*ii*) la croissance juvénile, plus particulièrement celle de la seconde année de vie, est un facteur important dans la détermination de la zone de croissance et les truites possèdent des comportements migratoires variables, allant de la résidence stricte au ruisseau natal jusqu'à la migration en mer, que l'on peut relier à leur taux de croissance juvénile et (*iii*) la description des tactiques d'histoire de vie (en incluant la croissance juvénile, le comportement migratoire à fine échelle et la reproduction) peut être affinée, les tactiques se distribuant le long d'un continuum temporel (age de reproduction) et spatial (distance de migration). La flexibilité des tactiques d'histoire de vie et leurs liens avec la croissance juvéniles sont confirmés dans cette étude. Cependant l'utilisation de données empiriques sur la croissance et la migration issues du marquage individuel par PIT tag a permis d'améliorer la description des tactiques en prenant en compte leur distribution continue dans le temps et l'espace.

Introduction

Salmonids are excellent models for testing predictions from evolutionary theory (global review in Hendry and Stearns 2003), e.g., alternative mating tactics (Gross 1985), evolution of reproductive traits (Kinnison et al. 2001; Olsen and Vøllestad 2003), evolution of migration (Gross 1987; Kinnison et al. 2003), and homing mechanisms (McDowall 2001). They are also particularly interesting because of the polymorphism of their life history tactics and migratory behaviour. This plasticity allows brown trout (*Salmo trutta*) to be the most ecologically variable and successful salmonid species (Jonsson 1989; Elliott 1994; Baglinière 1999). Here, the term "partial migration" is used to describe the phenomenon where a population splits into anadromous and resident individuals (Jonsson and Jonsson 1993). In these brown trout populations, present in coastal rivers (Jonsson 1985; L'Abbée-Lund et al. 1989), anadromous individuals migrate to the sea, whereas residents spend their entire life in fresh water. Migrant and resident adults can spawn successfully together (Jonsson 1985; Pettersson et al. 2001) and juveniles may grow up together and are indistinguishable during ontogeny, i.e., until migrants smoltify (Baglinière et al. 2000). The decision between anadromy and freshwater residence is

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J. Cucherousset,[1,2] D. Ombredane, K. Charles, and J.-L. Baglinière. Unité mixte de recherche, Institut national de la recherche agronomique (UMR INRA), Agrocampus Rennes, Ecobiologie et Qualité des Hydrosystèmes Continentaux, 65, rue de Saint-Brieuc, 35042 Rennes CEDEX, France.
F. Marchand. INRA, Unité Expérimentale d'Écologie et d'Écotoxicologie Aquatique, 65, rue de Saint-Brieuc, 35042 Rennes CEDEX, France.

[1]Corresponding author (e-mail: julien.cucherousset@univ-rennes1.fr).
[2]Present address: Université de Rennes 1, UMR 6553 ECOBIO, Campus de Beaulieu, Bât 25, 35042 Rennes CEDEX, France.

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an example of phenotypic plasticity and is influenced by both genetic and environmental factors (Jonsson and Jonsson 1993; Klemetsen et al. 2003).

The relationship between juvenile growth rate and migratory behaviour of brown trout has already been investigated (Jonsson 1985; Jonsson and Gravem 1985) but juvenile growth rate was usually estimated by back-calculation from scales or otoliths (e.g., Jonsson and Hindar 1982; L'Abée-Lund et al. 1989) and this may lead to errors of growth estimation (Berg and Jonsson 1990). The use of passive integrated transponders (PIT) is a method to acquire empiric data on growth (e.g., Vøllestad et al. 2002) because it allows for the individual marking of juveniles and the study of their entire life history (Prentice et al. 1990; Lucas and Baras 2000). As well, many studies on migration behaviour of brown trout have focused on anadromous versus freshwater resident individuals because the two forms were distinguished using morphological criteria (e.g., Jonsson 1985; Jonsson et al. 2001). Nevertheless, some resident fish exhibit freshwater migration (Baglinière et al. 1989; reviewed in Gowan et al. 1994) and these migrations were not integrated in the previous analyses of life histories. Owing to its characteristics, PIT technology allows monitoring of fine-scale movements (Armstrong et al. 1996; Greenberg and Giller 2000; Roussel et al. 2000) and freshwater migratory processes (Olsson and Greenberg 2004).

In the present study, we investigated the relationship between empiric growth rate, migratory behaviour including freshwater migrations, and life history tactics of wild brown trout from five consecutive cohorts of the Oir River population. Thus, we monitored 5900 age-0 PIT-tagged individuals during their entire life (i.e., 8 years of survey) and analysed life history tactics according to the empiric traits calculated from the long-term field survey.

Materials and methods

Studied population

The study was conducted on the Oir River (Normandy, France, 48°37′N, 1°16′W) brown trout population (Fig. 1). Eight kilometres from the sea (Le Mont-Saint-Michel Bay), the Oir River enters the Sélune River. The monitored area was located between Cerisel and Le Buat mills, including 13 km of the Oir River and the five largest tributaries (Moulin du Bois Brook, Sourvallée Brook, Roche Brook, Moulinet Brook (all second order), and Pont-Lévesque brook (third order)), each ranging from 3 to 6 km long.

The Oir River wild brown trout population has been studied since 1985 (e.g., Ombredane et al. 1998; Gouraud et al. 2001; Charles et al. 2004) and is composed of non-anadromous and sea-migratory individuals. The non-anadromous fish are present in the whole drainage from the small tributary to the main stream. The sea migratory part is mainly composed of finnocks (0+ year in the sea). The anadromous trout are mainly females (78.3%) and upstream migration starts in spring, but almost all of the fish enter the Oir River during fall. For both forms, reproduction occurs from the end of November to the middle of February within the tributaries and the upstream part of the Oir River. Furthermore, spawning grounds used by the two forms overlap (Charles et al. 2004).

Fish tagging and data acquisition

Between 1995 and 1999 (five cohorts), 5894 brown trout age-0 parr were captured in October using electrofishing, anaesthetized (phenoxy-2-ethanol), measured (fork length, ±1 mm), and PIT tagged in their natal brook. Tagging consisted of a PIT tag injection in the ventral part of the peritoneal cavity with a modified hypodermic syringe and a 2.7-mm-diameter sterile needle. The PIT tags used were 11.5 mm long and 2.12 mm in diameter and weighed 0.1 g in air (ID 100; EID Aalten B.V., Aalten, Netherlands). These small tags allow for monitoring small-bodied fish, i.e., >51 mm long. All fish were released into the river section from which they were captured (Ombredane et al. 1998). The five cohorts were monitored during 8 years (from 1995 to December 2002). This allowed all 1999 cohort individuals to spawn at least once. Monitoring was performed using three different methods. First, once a year in October, all of the brooks and the Oir River were electrofished by wading using generator-powered electrofishing gear (type Héron; Dream electronique, France). The same sections homogeneously distributed in the drainage basin were sampled every year, totaling 6490 m. Roche Brook and Moulinet Brook (1850 m) were also sampled in May. During the spawning period, adults were electrofished on the spawning areas located in the brooks and the upstream part of the Oir River using a backpack electrofishing unit (type Martin-Pêcheur; Dream electronique, France). Second, an upstream and downstream trapping system was continuously functioning during the entire study at the Cerisel mill (Fig. 1). These traps captured migratory fish that enter or leave the Oir catchment basin. During two winters (1996 and 1997), an upstream trap was placed at the mouth of La Roche Brook to capture spawners. For each trout trapped, PIT tagging was verified and fork length (±1 mm) measured. Scales were removed (age determination, growth patterns, and spawning checks) and a phenotypic description performed (smolting for juveniles, silvering and sexual maturation for adults) (Baglinière et al. 2000). Third, flat-bed antennae (1000 mm × 350 mm × 25 mm) (U.K.I.D. Systems Ltd., Preston, UK) used in conjunction with decoders and data loggers (SPD and HPSPD; U.K.I.D. Systems Ltd.) were placed in each tributary mouth and at the Cerisel mill (Fig. 1). This allowed for the detection of PIT-tagged fish movements and the recording of the day and hour of the displacement (Armstrong et al. 1996; Lucas and Baras 2000). On the brooks, two adjacent antennae were installed to determine displacement direction.

Life history traits and statistical analysis

The data collected during 8 years in the field (tagging, recapture, and antennae recording) were gathered to calculate life history traits for each tagged brown trout (Table 1). From all of the PIT-tagged fish (type 1), some individuals (type 2) were recorded growing either in their natal brook, in the Oir River, in the Sélune River, or in the sea, whereas others (type 3) were monitored until reproduction (i.e., detected as mature, captured in spawning areas, or monitored during an upstream migration to the spawning areas). Indeed, at least 69% of the fish caught before the reproduction in the upstream trap at the mouth of La Roche Brook and 96% of

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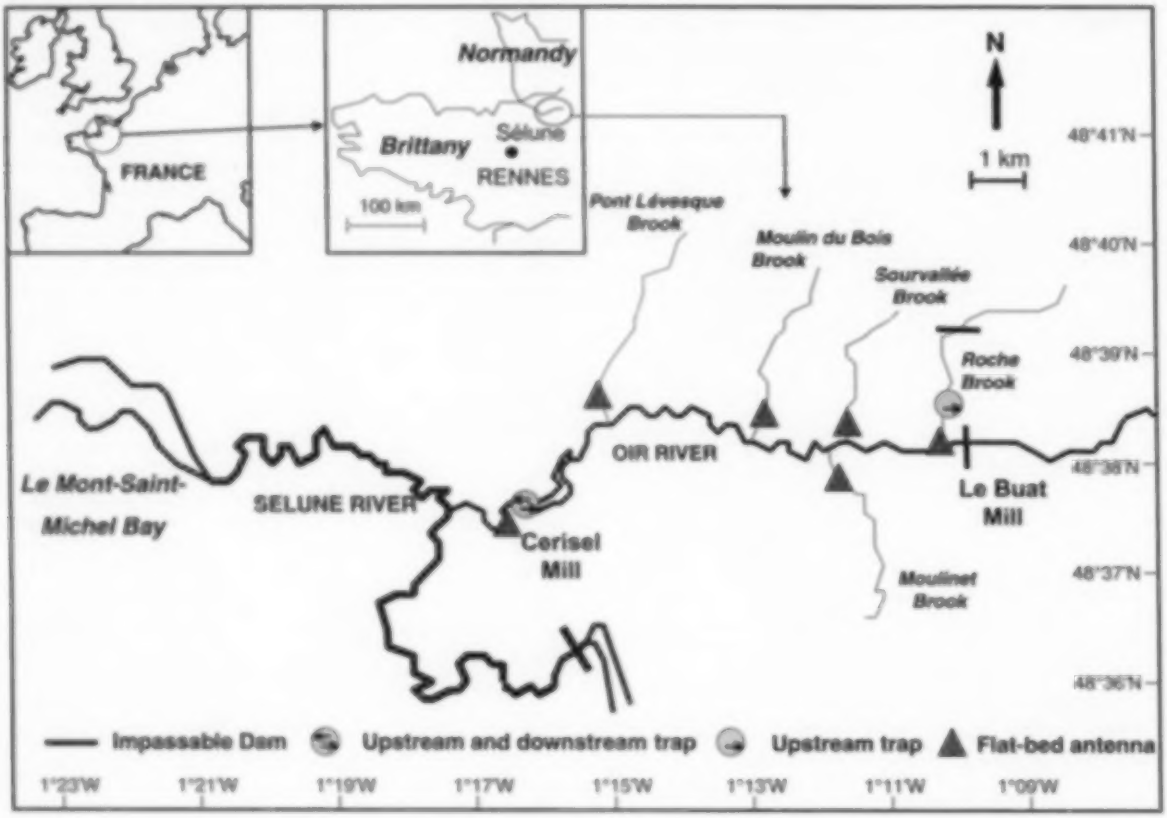
Fig. 1. Map of the study site in the Oir River basin, France. Brown trout (*Salmo trutta*) were captured, tagged with passive integrated transponders, and monitored between Le Buat and Cerisel mills, including the five largest tributaries. Thick lines, circles, and triangles indicate impassable dams, traps, and flat-bed antennae, respectively.



those recaptured in spawning areas were mature. Furthermore, all trapped finnocks were detected as mature.

We tested for differences in life history traits between fish monitored until reproduction and the others (no reproduction observed) and between cohorts for all of the PIT-tagged individuals. Assumptions of normality and homoscedasticity were tested using the Kolmogorov–Smirnov/Lilliefors test (1967) and the Levene test, respectively. A series of one-way analysis of variance (ANOVA) was performed for single comparisons, whereas multiple comparisons were performed using post hoc Tukey pairwise procedures for parametric ANOVA. When deviations from normality were detected, life history trait variability was investigated with the nonparametric Kruskal–Wallis test and Mann–Whitney *U* test. These statistical analyses were performed using SYSTAT 9 (SPSS Inc., Chicago, Illinois). A rejection level of 0.05 was used in all tests.

An intercohort variability in life history traits was detected. Data were standardized (centred and normalized; Legendre and Legendre 1998) to combine all of the individuals of the five cohorts to investigate of migratory behaviour and life history tactics. Since a majority of life history traits were qualitative (Table 1), quantitative data were converted into qualitative data to homogenize the data set. Five categories (very low, low, intermediate, high, and very high) were used, each with a similar number of individuals (see details in Escofier and Pages 1988). Multiple correspondence analyses (MCA) were performed on life history traits followed by a hierarchical ascending classification (HAC) using individual factorial scores of the MCA principal axes to create patterns (Lebart et al. 1984; Tenenhaus and Young 1985). The analyses were performed using the empiric traits (Table 1) related to juvenile growth (fork length at age 0 (0+FL) and growth rate between age 0 and age 1 (GR0+1+)), migration (growing environment (GE), age at migration from the natal brook (AMNB), age at migration from the Oir River (AMOR) with the associated fork length (FLMOR), and age at smoltification (AS) with the associated fork length (FLS)), and reproduction (age at maturity (AM), fork length at maturity (FLM), type of reproduction schedule (NR), and sex). The multivariate analyses were performed with SPAD 4.5 (CISIA, Montreuil, France).

Results

Tagging data

During the 8 years of fieldwork (1995–2002), 5894 brown trout parr (type 1) were PIT tagged from 699 to 1759 individuals per cohort. For the entire period of the study, 36.7% of the tagged fish were recaptured at least once (electro-

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Table 1. List of the life history traits measured for the study.

Abbreviation	Description	Calculation	Units	Category[a]	Transformation from quantitative to qualitative performed
0+FL	Fork length at age 0	Size in October when the individual was caught for the first time and PIT tagged	mm	JG	Yes
GR0+1+	Growth rate between age 0 and age 1	GR0+1+ = $(FLb - FLa)(Db - Da)^{-1}$; FL, fork length; D, capture date; *a*, capture at age 0; *b*, recapture at age 1	mm·day^{-1}	JG	Yes
GE	Growth environment	Environment of subadult growth (brook, Oir River, Sélune River and Sea)	—	M	No
AMNB	Age at migration from the natal brook	Age when migrating downstream and recorded at the antennae of the natal brook	years	M	No
AMOR	Age at migration from the Oir River	Age when trapped and (or) recorded at the Cerisel mill (Oir River mouth)	years	M	No
FLMOR	Fork length at migration from the Oir River	Size when trapped at the Cerisel mill (Oir River mouth)	mm	M	Yes
AS	Age at smoltification	Age when trapped as a smolt or calculated from the scales of anadromous adults	years	M	No
FLS	Fork length at smoltification	Size when trapped as a smolt in Cerisel mill (Oir River mouth)	mm	M	Yes
AM	Age at maturity	Age when migrated upstream or detected as mature for the first time	years	R	No
FLM	Fork length at maturity	Size in October before the first participation in reproduction	mm	R	Yes
NR	Type of reproduction schedule	Split into semelparous (death after spawning) and iteroparous (multispawner)	—	R	No
Sex	Sex	Determined using morphological and physiological criteria for mature fish	—	R	No

[a]JG, juvenile growth; M, migration; R, reproduction. A dash means that the life history trait is expressed without units.

fishing, trapping, or antennae recording), ranging from 21.2% to 41.0% depending on the cohort. Among all tagged fish, 21.9% (n = 1288, type 2) were monitored growing either in their natal brook, in the Oir River, in the Sélune River, or in the sea. Finally, 7.4% (n = 435, type 3) of the tagged fish were monitored until reproduction (Table 2).

Juvenile life history trait variability

Fish that were lost before maturity (reproduction unobserved) grew slowly between age 0 and age 1 (ANOVA, $p < 0.05$) and moved from the Oir River at an earlier age (Mann–Whitney U test, $p < 0.05$) than those fish monitored breeding in the system (reproduction confirmed) (Fig. 2). In all life history traits, significant differences (ANOVA and Kruskal–Wallis test, $p < 0.05$) exist between cohorts (Table 3) but none between brooks. The 1997 cohort had significantly the smallest values, and the 1995 cohort had the largest (ANOVA followed by Tukey's test, $p < 0.05$).

Relationship between juvenile life history traits and the growing environment

Using the four most informative axes of the MCA (percent inertia = 37.24% cumulated) that was performed with four active variables (0+FL, GR0+1+, GE, and sex) and three supplementary variables (AMNB, AMOR, and FLMOR), five individual patterns (inter-/intra-inertia ratio = 59%) (Fig. 3) were recognized by HAC. Fish that spent their entire life in their natal brook were chiefly males. They were either (*i*) very small at the end of the first and second year or (*ii*) very fast growers at the end of the first and second year. (*iii*) Many females smolted and moved to grow in the sea at age 2. They grew quickly during the first year but exhibited intermediate growth during the second year in fresh water. (*iv*) Some fish of both sexes with intermediate first-year growth moved downstream to spend the second year as fast growers in the Oir River. (*v*) Some fish of both sexes with high first-year growth moved downstream at age 1 to grow up in the Sélune River.

Life history tactics in light of reproduction-authenticated fish

Using the three most informative axes of the MCA (percent inertia = 46.35% cumulated) that was performed with four active variables (GE, sex, AM, and FLM) and seven supplementary variables (AMNB, AMOR, AS, FLS, FLMOR, NR, 0+FL, and GR0+1+), five individual patterns (inter-/intra-inertia ratio = 89%) (Fig. 4) were recognized by the HAC. (*i*) Some trout spent their entire life in the brook;

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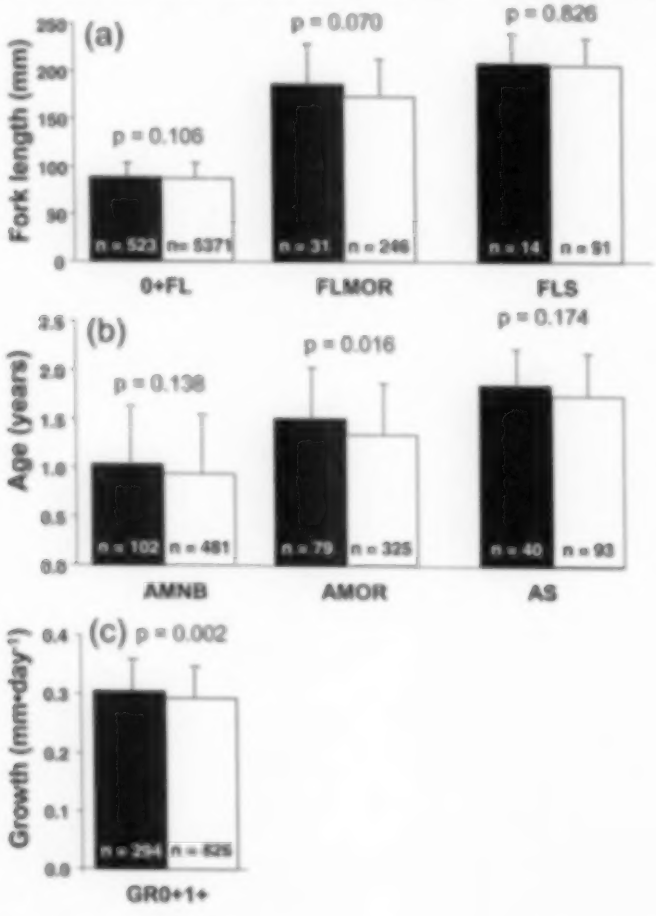
Table 2. Data collected per cohort and in total on passive integrated transponder (PIT)-tagged brown trout (*Salmo trutta*) from 1995 to 2002.

Cohort	*n*	0+FL	Recaptured fish	Growing environment documented	Reproduction confirmed
1995	746	88.8 (±15.1)	297 (39.8%)	189 (25.3%)	51 (6.8%)
1996	1619	85.1 (±14.4)	663 (41.0%)	400 (24.7%)	113 (7.0%)
1997	1759	82.7 (±14.7)	601 (34.2%)	339 (19.3%)	143 (8.1%)
1998	699	93.2 (±13.8)	183 (21.2%)	76 (10.9%)	26 (3.7%)
1999	1071	96.1 (±17.5)	419 (39.1%)	284 (26.5%)	102 (9.5%)
Total	5894	87.8 (±15.9)	2163 (36.7%)	1288 (21.9%)	435 (7.4%)

Note: *n* is the number of tagged individuals. Data for fork length at age 0 (0+FL) are means (±SD). The proportion (%) within the number of PIT-tagged fish for recaptured fish (electrofishing, trapping, and (or) antenna recording) and growing-environment-documented and reproduction-authenticated individuals is given in parentheses.

Fig. 2. Comparison of juvenile brown trout (*Salmo trutta*) life history traits between reproduction-confirmed (solid bars) and reproduction-unobserved individuals (open bars). (*a*) Fork length: 0+FL, fork length at age 0; FLMOR, fork length at migration from the Oir River; FLS, fork length at smoltification. (*b*) Age: AMNB, age at migration from the natal brook; AMOR, age at migration from the Oir River; AS, age at smoltification. (*c*) Growth rate: GR0+1+, growth rate between age 0 and age 1. Error bars are standard deviation.



their mean life span was 3 years but few data were available on their reproduction. (*ii*) Other fish migrated downstream from the brook at age 1, grew in the Oir River, and spawned the first time at 3 years old. They had an intermediate and high size and generally died after spawning. (*iii*) Many males grew as subadults in the Oir River and reproduced once at age 2 with an intermediate size. (*iv*) Some females migrated downstream at either age 1 or age 2, grew in the sea, and spawned for the first time at age 3. Usually, these fish had very large size and were multispawners. (*v*) Some

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Table 3. Mean (±SD) values of juvenile brown trout (*Salmo trutta*) life history traits used to investigate yearly variability for the five cohorts.

Cohort	Trait 0+FL	GR0+1+	FLMOR	FLS	FLM	AMNB	AMOR	AS	AM
1995	88.75 (±15.08)	0.27 (±0.06)	196.21 (±42.06)	215.65 (±27.50)	238.30 (±58.50)	1.74 (±0. 45)	1.68 (±0. 47)	2.00 (±0.00)	2.59 (±0.66)
1996	85.11 (±14.39)	0.28 (±0.05)	179.35 (±38.27)	210.28 (±22.94)	216.29 (±61.64)	0.99 (±0. 53)	1.64 (±0. 48)	1.93 (±0.26)	2.58 (±0.66)
1997	82.68 (±14.67)	0.32 (±0.05)	144.30 (±30.87)	222.00 (±43.50)	212.98 (±90.40)	0.74 (±0. 59)	1.13 (±0. 45)	1.82 (±0.40)	2.32 (±0.85)
1998	93.08 (±13.66)	0.28 (±0.06)	203.18 (±30.10)	213.47 (±23.69)	231.76 (±54.12)	1.07 (±0. 65)	1.62 (±0. 64)	1.94 (±0.24)	2.51 (±0.56)
1999	96.08 (±17.48)	0.33 (±0.05)	166.60 (±29.60)	192.23 (±32.82)	251.29 (±55.56)	1.01 (±0. 59)	1.12 (±0. 33)	1.25 (±0.44)	2.50 (±0.50)

Note: 0+FL, fork length at age 0; GR0+1+, growth rate between age 0 and age 1; FLMOR, fork length at migration from the Oir River; FLS, fork length at smoltification; FLM, fork length at maturity; AMNB, age at migration from the natal brook; AMOR, age at migration from the Oir River; AS, age at smoltification; AM, age at maturity.

fish, staying in the natal brook or migrating downstream from the brook at age 0, reproduced at age 1. They spawned with a very small size and were mainly semelparous individuals.

A diagram representing the principal life history of the Oir River wild brown trout population was formulated using the results of the analyses of empiric life history traits related to juvenile growth, migration, and reproduction (Fig. 5). In light of these results, the overall life history tactics present a continuous gradient in time (life cycle duration) and space (growth from the natal brook until the sea).

Discussion

This approach is novel because it examines empiric life history traits coming from a study using long-term individual data, i.e., from a massive PIT tagging of five cohorts and their monitoring during their entire life. This study confirms and demonstrates that (*i*) juvenile life history traits present a yearly variability and some traits tend to be higher for those fish monitored until reproduction, (*ii*) juvenile growth, particularly GR0+1+, plays an important role in the determination of the growing environment, and (*iii*) life history tactics cannot be classified solely as anadromous and resident individuals and can be described more precisely. We detected that when freshwater migrations are taken into account, life history tactics are expressed along a spatial and temporal continuum.

Juvenile life history trait variability

Juvenile growth tended to be higher for those fish monitored until reproduction in comparison with those fish lost during the survey. With regard to the high recapture effort (electrofishing, antennae, and trapping) and the very low level of PIT tag loss (Ombredane et al. 1998), fish lost during the survey certainly do not survive and never spawn. This result confirms the classical knowledge that early life history traits influence fitness by affecting survival probability later in life (e.g., Chadwick and Claytor 1990; Einum and Fleming 2000; Pakkasmaa and Jones 2002). Nevertheless, the absence of significant differences between groups could be explained with reference to the disproportion between sample sizes. Indeed, the number of fish monitored until reproduction fish is smaller owing to the effect of natural mortality from tagging (age 0) until the individual reaches maturity. As well, the analysis of finer parameters such as energy status or instantaneous growth rate (Forseth et al. 1999) might allow detection of the differences between these individuals.

A yearly variability, particularly in 1995 and 1997 cohorts, was detected for all traits calculated in the present study, highlighting the environmental influence on life history traits, such as growth rate (Näslund 1993). Environmental factors will act at two levels: (*i*) the river basin level, where temperature and water flow will affect the entire population and create intercohort variability (L'Abée-Lund et al. 1989; Jonsson and L'Abée-Lund 1993; Lobón-Cerviá and Rincón 1998), and (*ii*) the river section level, where habitat quality (Heggenes et al. 1999; Roussel and Bardonnet 2002), resource availability (Heggenes et al. 1995), and competition (Heggenes et al. 1999; Nordwall et al. 2001; Harwood et al.

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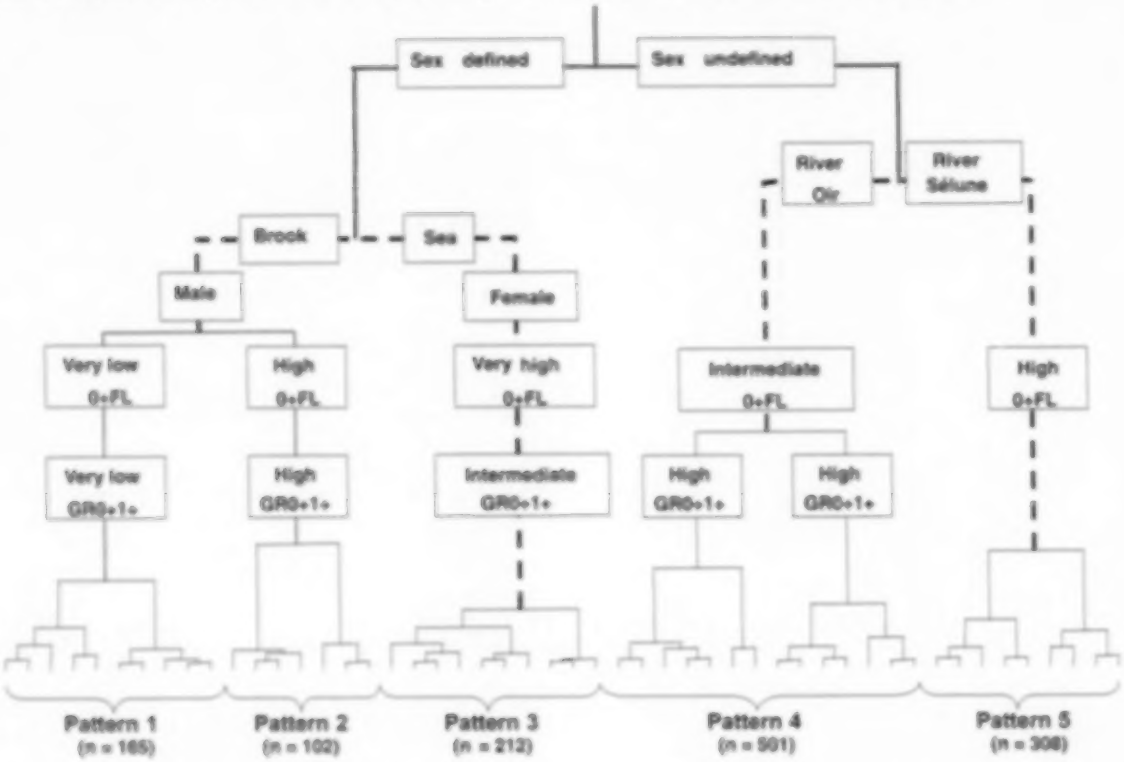
Fig. 3. Distribution of passive integrated transponder (PIT)-tagged brown trout (*Salmo trutta*) (type 2) within the patterns (*n* individuals) regarding the determination of growing environment in a hierarchical ascending classification. The composition of the patterns can be seen following the tree diagram. Sex was qualified as undefined when both sexes were present in the pattern and as defined when only one sex occurred in the pattern. 0+FL, fork length at age 0; GR0+1+, growth rate between age 0 and age 1.



2002) will affect the individual and create intracohort variability. In future studies, the influence of environmental conditions on life history traits should be thoroughly investigated at a finer scale and included in the study of life history tactics.

Migration behaviour and the migration continuum concept

This paper underscores that juvenile growth and metabolic rate play a major role in the determination of the growing environment (Forseth et al. 1999) and demonstrates that GR0+1+, calculated from PIT-tagging data, may allow clarification of this role. Thus, individuals with a low energetic rate remained in the environment in which they were born because it can be sustained in the brook (pattern 1). Trout, whose metabolic needs were higher, left the brook to migrate to the Oir River. If they were able to maintain their growth rate during their second year (expressed by a high GR0+1+), these fish remained in the Oir River (pattern 4). If they did not satisfy their high metabolic rate (expressed by lower GR0+1+), they extended their downstream migration outside the Oir system in the Sélune River (pattern 5) or as far as the sea (pattern 3). There were sexual differences for individuals with very high 0+FL. Males tend to remain in the brook (pattern 2), whereas females migrate to the sea (pattern 3). Juvenile brown trout appear to migrate from one habitat to another as a phenotypically plastic response to declining growth performance as they reach a threshold in their present habitat owing to environmental conditions. The sources of variation in metabolic rates among individuals are uncertain, but maternal and developmental effects might cause such variation (Forseth et al. 1999).

With regard to our PIT tagging data, fish that migrate in the river were monitored growing from the upper part to the river mouth and clearly grew in a spatial continuum from the natal brook to the sea, including the entire drainage. To understand such complex mechanisms, we should interpret migrations not only with reference to their distance and the salinity of the environment that they traverse but with an ecological and biological viewpoint. The migration continuum concept (Lucas and Baras 2001) is a new way to investigate such complex phenomena. Migration, whatever the distance and environment travelled (Lucas and Baras 2001), is likely to be dependent on a trade-off between benefits and costs of the environment (Jonsson and Jonsson 1993). The access to environment with higher production may have to be balanced by unfavourable conditions, such as an increased mortality rate or osmoregulation changes (Northcote 1992; Jonsson and Jonsson 1993). Thus, the food availability hypothesis (Gross et al. 1988) is a relevant way to understand why fish migrate. As partial migration in a population evolved in response to resource availability in a changing

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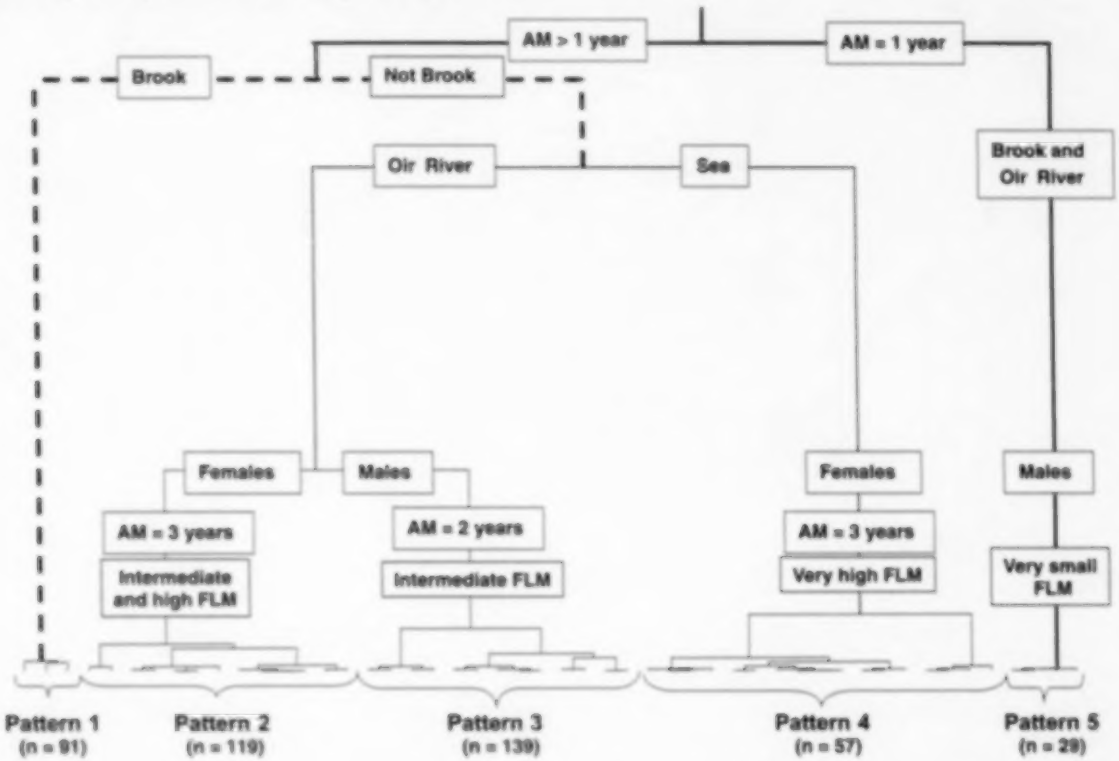
Fig. 4. Distribution of passive integrated transponder (PIT)-tagged brown trout (*Salmo trutta*) (type 3) within the life history tactic patterns (*n* individuals) in a hierarchical ascending classification. The composition of the patterns can be seen by following the tree diagram. AM, age at migration; FLM, fork length at migration.



habitat (Jonsson and Jonsson 1993), it would be of interest to investigate how human impacts on environment might affect migratory processes. This new emphasis is especially valid with regard to these results. Reconsidering the significance of migration in reference to the migration continuum concept and environmental effects is key to resolving the complexity of the brown trout migratory process and its variability among individuals and populations.

A spatial and temporal continuum of life history tactics

In the population that we studied, we clarify the description of life history tactics by analysing empiric growth and including freshwater migration and detect that tactics are expressed along a continuous gradient. Precocious males, reproducing at age 1, spent their entire life in the nursery brook, some of them with a brief passage in the river (pattern 5). They exhibited strong juvenile growth rate, and maturation rate is positively correlated with first-year growth (Baglinière and Maisse 2002). They participate in reproduction as satellites because they are unable to defend a reproductive territory but may fertilize some of the eggs of the females that are spawning primarily with larger males (Gross 1985; Bohlin et al. 1990; Jonsson and Jonsson 1993). Thus, the size advantage attained in the brook, relative to slower-growing individuals, may be converted into a fitness advantage. Others males grew in the Oir River and reproduced at age 2 (pattern 3). We also observed slower-growing individuals, which remained in the brook for their entire life (pattern 1). We also found individuals that migrate and grow in the Oir River. They exhibited an intermediate juvenile growth rate and reproduced at age 3 (pattern 2). Some females were found migrating outside the Oir River (Sélune River and Sea) and reproducing when they were age 3, as large bodied-size individuals, and were fast-growing juveniles (pattern 4). Migration advantages, such as an increase of food availability (Gross et al. 1988), might enhance their fitness because female fitness is strongly dependent on their size. Selection seems to favour rapid growth and large body size in females (Jonsson and Jonsson 1993). Nevertheless, some alternative tactics were present within the population, such as males growing in the Sélune River and spawning at age 3. Because of their low frequency, these tactics were not isolated by HAC.

Brown trout males achieve their reproductive success in fresh water after few years of growth (Baglinière et al. 2001), while some of them choose the precocious sexual maturation strategy (detailed in Bohlin et al. 1990; Dellefors and Faremo 1988). Females, whose fitness is strongly dependent on their size (Jonsson and Jonsson 1993), reproduce at older ages than males (Baglinière and Maisse 2002). Since they have higher energetic needs to mature (Euzenat et al. 1999), selection tends to favour faster-growing females (Jonsson and Jonsson 1993), which will need to migrate to more productive environments. Such results confirm previous obser-

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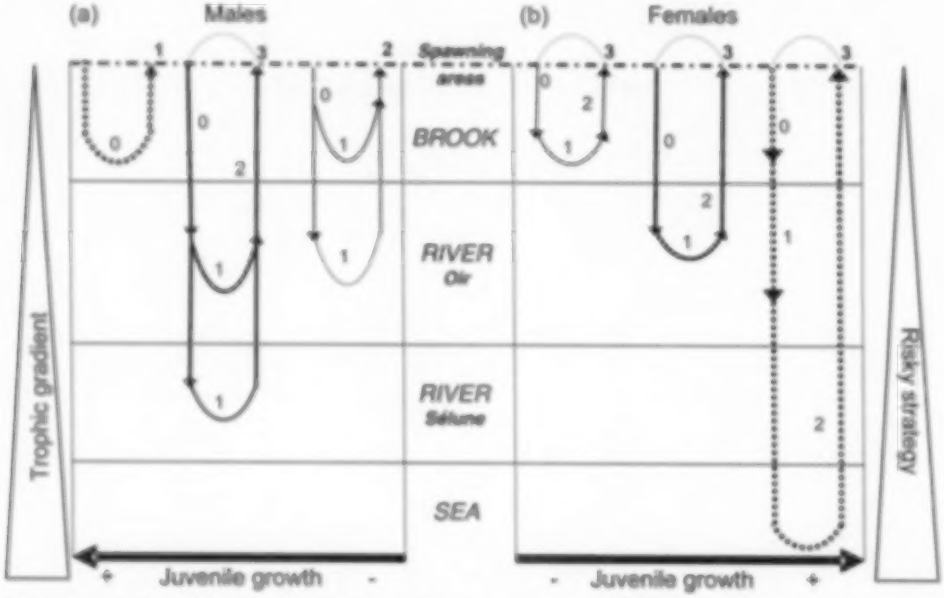
Fig. 5. Continuum of life history tactics in the Oir River brown trout (*Salmo trutta*) population: (*a*) males and (*b*) females. In the middle are the different environments in which fish live, migrate, grow, and spawn. A gradient of juvenile growth (first and second years; numbers on inside of graphic) increasing from the centre to the edge is shown below: the thin solid line, thick solid line, and thick broken line represent low, intermediate, and high juvenile growth rate, respectively. An arrow represents 1 year. Numbers along the top indicate age at maturity. A thin dotted line completing the life cycle is present when most of the fish survived after spawning (multispawners).



vations that males often predominate among freshwater fish and females among anadromous fish (Jonsson and Jonsson 1993). Nevertheless, whatever the life history tactic is, both sexes are represented. The existence of these alternative tactics provides a selection advantage in a fluctuating environment and when only one ecological niche does not allow for maximizing population fitness (Northcote 1992; Jonsson and Jonsson 1993). This phenotypic plasticity will be favoured as long as individuals can produce polymorphic offspring that have more viable progeny than those without this opportunity (Northcote 1992; Jonsson and Jonsson 1993).

In conclusion, the classical conception of life history tactics in brown trout, opposing only extremes of anadromous versus freshwater resident individuals, can be clarified by analysing empiric data related to growth and reproduction in conjunction with fine-scale migration. Because (*i*) brown trout is a highly polymorphic and ecologically variable species (Jonsson 1989; Elliott 1994; Baglinière 1999), (*ii*) life history traits are phenotypically plastic in response to environment and genetic parameters (Jonsson et al. 2001), and (*iii*) aquatic ecosystems present a continuous gradient of physical conditions (river continuum concept; Vannote et al. 1980), brown trout can exhibit a continuum in time and space of life history tactics to optimize individual fitness and population persistence.

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Predation on winter flounder (*Pseudopleuronectes americanus*) eggs by the sand shrimp (*Crangon septemspinosa*)

David L. Taylor and Donald J. Danila

Abstract: This study estimated rates of sand shrimp (*Crangon septemspinosa*) predation on winter flounder (*Pseudopleuronectes americanus*) eggs and examined the effect of temperature on density-dependent mortality of early-stage flounder. In laboratory experiments, shrimp feeding rates on flounder eggs were positively correlated with temperature and shrimp size. Immunological assays of shrimp stomach contents indicated that 7.2% of shrimp collected from the Niantic River (Connecticut) had flounder eggs in their stomachs. Incidence of egg predation was highest in February (20%) and decreased continuously into early April (1.2%). In a deterministic model simulating predator-induced mortality of flounder eggs during a spawning season, shrimp consumed 0.4%–49.7% of the total flounder spawn. Variations in shrimp population abundance and size structure accounted for the greatest variability in egg mortality. Water temperature during the spawning season presumably alters the population dynamics of early-stage flounder. In a long-term survey, the number of yolk-sac flounder larvae in warm years (≥4.3 °C) was depressed at high egg densities, indicating strong compensatory processes that increased egg mortality and limited the abundance of larvae. Failure of flounder to produce strong year-classes of larvae during warm years, possibly resulting from altered trophic dynamics, may explain the inability of stocks to recover from previous overexploitation.

Résumé : Nous estimons dans notre étude les taux de prédation de la crevette des sables (*Crangon septemspinosa*) sur les oeufs de la plie rouge (*Pseudopleuronectes americanus*) et évaluons les effets de la température sur la mortalité dépendante de la densité chez les premiers stades de la plie. Dans des expériences de laboratoire, il y a une corrélation positive entre les taux d'alimentation des crevettes sur les oeufs de plie, d'une part, et la température et la taille des crevettes, d'autre part. Des tests immunologiques sur les estomacs des crevettes récoltées dans la Niantic (Connecticut) révèlent que 7,2 % des estomacs contiennent des oeufs de plie. La fréquence de la prédation des oeufs est maximale en février (20 %) et décroît graduellement jusqu'au début d'avril (1,2 %). Un modèle déterministe qui simule la mortalité des oeufs de plie due aux prédateurs durant la saison de reproduction indique que les crevettes consomment 0,4–49,7 % de l'ensemble de la ponte des plies. Les variations d'abondance et la structure de taille de la population de crevettes expliquent la plus grande partie de la variabilité de la mortalité des oeufs. La température de l'eau durant la saison de reproduction modifie sans doute la dynamique de population des plies de premiers stades. Dans une étude à long terme, le nombre de larves vésiculées de plies, les années d'eau plus chaude (≥4,3 °C), est réduit aux fortes densités d'oeufs, ce qui indique qu'il y existe d'importants processus compensatoires qui augmentent la mortalité des oeufs et limitent l'abondance des larves. L'incapacité des plies à produire des classes d'âge plus importantes les années chaudes, qui résulte peut-être d'un changement trophodynamique, peut expliquer pourquoi les stocks ne réussissent pas à se remettre de la surexploitation du passé.

[Traduit par la Rédaction]

Introduction

Understanding the population dynamics of marine fish stocks requires insight into the sources of mortality that affect the early life history stages of fish. The principal biotic factors contributing to the mortality of early-stage fish include variations in food availability, resource competition, and predation (Anderson 1988; Bailey and Houde 1989 and references therein). Although starvation can be a direct source of larval mortality during the transition to exogenous feeding, it does not explain the substantial losses incurred during the egg and yolk-sac larval life stage. Therefore, predation is recognized as the most important source of mortality for fish eggs and larvae that rely on endogenous food resources (Bailey and Houde 1989).

The eggs of demersal spawners are particularly susceptible to high rates of mortality from epibenthic predators (Tay-

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D.L. Taylor.[1] Department of Biology and Marine Biology, Roger Williams University, 1 Old Ferry Road, Bristol, RI 02809, USA.
D.J. Danila. Millstone Environmental Laboratory, Dominion Nuclear Connecticut, Inc., Millstone Power Station, P.O. Box 128, Waterford, CT 06385, USA.

[1]Corresponding author (e-mail: dtaylor@rwu.edu).

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lor 1964; Frank and Leggett 1984; Haegele 1993). Severe predatory losses of demersal eggs may contribute to the evolution of several survival strategies that reduce or compensate for intense mortality and thus promote the survival of recruits. Adopted reproductive strategies include high fecundity of spawners (Buckley et al. 1991*a*, 1991*b*), deposition of eggs in substrates or attachment to macrophytes to provide refugia (Frank and Leggett 1984; Fuiman 2002), parental care and nest defense (Wisenden 1999; Asoh and Yoshikawa 2001; Skolbekken and Utne-Palm 2001), unpalatable eggs (Gladstone 1987), and discrete spawning events that confer a spatial and temporal refuge from potential oophagous predators (Frank and Leggett 1984, 1985; Holt et al. 1985).

The winter flounder (*Pseudopleuronectes americanus*) is a pleuronectid flatfish inhabiting temperate waters of the northwest and mid-Atlantic (Collette and Klein-MacPhee 2002). The historical dominance of winter flounder within its geographic range has been attributed to a unique life history relative to other demersal fishes (Jeffries and Terceiro 1985; Jeffries et al. 1989). Winter flounder are reproductively active during the winter and early spring (January to April), at which time adult male and female flounder migrate into estuaries in ripe spawning condition (Stoner et al. 1999; Collette and Klein-MacPhee 2002). Winter flounder are batch spawners, releasing a single brood of oocytes over a period of at least 1 week (Burton and Idler 1984; Stoner et al. 1999). The adhesive, demersal eggs of winter flounder are spawned in shallow water (1.8–5.4 m) at temperatures ranging from 1 to 10 °C with peak spawning occurring at 2–5 °C (Collette and Klein-MacPhee 2002). During the incubation period lasting several days to weeks (Rogers 1976), clusters of winter flounder eggs could experience substantial mortality owing to epibenthic predation. By virtue of winter flounder spawning at cold temperatures in shallow estuaries, however, the flounder obtain a survival advantage because of the presumably low abundance and activity of potential predators.

Winter flounder have traditionally supported valuable commercial and recreational fisheries along the northeastern United States (Northeast Fisheries Science Center 2003). The New England – mid-Atlantic winter flounder stock complex has experienced dramatic cyclical changes in population abundance, with adults known to fluctuate sevenfold within a decade (Jeffries and Terceiro 1985). Concerns currently exist because regional subpopulations of this fish stock have declined precipitously since the early 1980s and have yet to rebound during the last two decades (Northeast Fisheries Science Center 2003). Concurrent with the dramatic decline in localized winter flounder populations is a significant warming trend in many northwest Atlantic estuaries (Keller and Klein-MacPhee 2000). Several investigators have proposed that elevated temperatures alter complex trophic interactions causing marked shifts in species composition (Jeffries and Terceiro 1985; Murawski 1993). For example, numerous studies document an inverse relationship between winter water temperature and the recruitment success of winter flounder, where the synergistic effects of climatic warming and predator–prey dynamics are thought to be the primary factors regulating the abundance of early-stage flounder (Jeffries and Terceiro 1985; Keller and Klein-MacPhee 2000). The decline in winter flounder abundance, coupled with changes in climate conditions, has raised the question of whether these previously overexploited stocks can recover in the face of altered trophic dynamics.

The adverse effect of increasing temperature on the survival of early-stage winter flounder is possibly related to the additional effect of temperature on the behavior and physiology of potential crustacean predators. In particular, the sand shrimp (*Crangon septemspinosa*) is a common estuarine decapod distributed along the northwestern Atlantic from Newfoundland to eastern Florida; hence, the shrimp spatially overlaps with the geographic distribution of winter flounder (Price 1962; Haefner 1979). Elevated water temperatures may enable sand shrimp to reside in estuaries year-round, thus foregoing the shrimp's offshore migration during late fall and early winter and creating a spatial and temporal overlap with the spawning of winter flounder eggs in winter and early spring (Boddeke 1976; Temming and Damm 2002). Moreover, increased temperature could directly influence the physiology of sand shrimp by accelerating metabolic activity and subsequently the consumption rate of shrimp (Keller and Klein-MacPhee 2000; Taylor and Peck 2004). There is also evidence suggesting that processes affecting the survival of the early life history of flatfish are critical determinants of year-class strength (Bailey 1994); hence, the effect of temperature on shrimp predation on winter flounder eggs warrants further investigation.

Difficulties in assessment have hampered our understanding of how predation affects the early life stages of fish. Visual estimates of a predator's stomach contents have traditionally been used to elucidate trophic linkages under field conditions (Wilcox and Jeffries 1974). However, quantifying predatory impacts is particularly difficult when analyses rely on visually identifying the remnants of soft-bodied prey, such as fish eggs, in the stomachs of suspected predators. Direct observations of crustacean diets are especially challenging because mandible and gastric mill grinding macerates prey and renders fish tissue visually unidentifiable. Immunological assays offer an alternative approach for dietary analyses and have been used to successfully identify the stomach contents of several marine crustaceans, including crangonid shrimp (Brodeur and Merati 1993; Van der Veer et al. 1998). Moreover, serological techniques have proven useful in assessing the contribution of crustacean predators to the total mortality suffered by the eggs of walleye pollock (*Theragra chalcogramma*) (Bailey et al. 1993; Brodeur and Merati 1993) and anchoveta species (*Engraulis mordax* and *Engraulis ringens*) (Theilacker et al. 1986, 1993; Krautz et al. 2003).

In a recent study, Taylor (2004) developed winter flounder specific antiserum that successfully identified egg proteins in the stomach contents of sand shrimp. Moreover, preliminary analysis of the diet of field-collected sand shrimp revealed that they are predators of winter flounder eggs in natural populations (Taylor 2004). This paper attempts to quantify the relative importance of sand shrimp predation on winter flounder eggs and the potential effects of winter water temperature on flounder year-class strength and recruitment. In laboratory experiments, we quantified shrimp feeding rates on winter flounder eggs as a function of water temperature, shrimp body size, and shrimp reproductive status. Results

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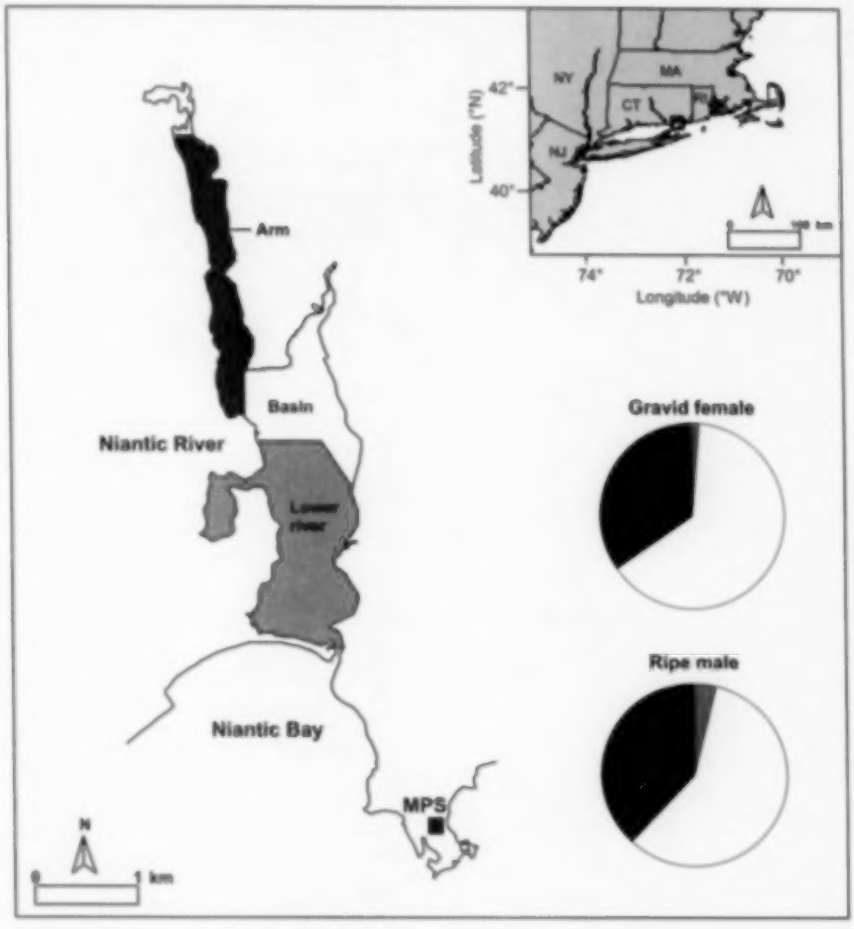
Fig. 1. Map of the Niantic River, Connecticut, demarcating three primary sections of the river: arm, basin, and lower river. Pie diagrams illustrate the proportion of total catch of reproductive winter flounder (*Pseudopleuronectes americanus*) (>26 cm TL) relative to river location. The adult flounder survey began on 18 February and concluded on 1 April 2002. MPS is the Millstone Power Station (Waterford, Connecticut) located on Niantic Bay.



from feeding experiments and stomach content analysis of field-collected shrimp were incorporated into a deterministic model, which in turn simulated the predator-induced mortality of flounder eggs during a defined spawning season. Finally, the effect of winter water temperature on the population dynamics of early-stage flounder was examined and discussed relative to the potential effects of climate-induced changes in the trophic system. Assessing climatic impacts on winter flounder population dynamics, mediated through predator–prey interactions, is necessary to address the question of what factors limit the recovery of these stocks from previous overexploitation.

Materials and methods

Laboratory feeding experiments

Shrimp used in laboratory feeding experiments were collected by otter trawl during late fall and winter from the Niantic River, Connecticut (Fig. 1). Shrimp were transferred to the laboratory where they were maintained in large flow-through tanks and fed frozen hard clam (*Mercenaria mercenaria*) and blue mussel (*Mytilus edulis*) ab libitum each day. Laboratory conditions were maintained at winter and early spring ambient levels (temperature = 2–10 °C, salinity = 28–30 ppt). Similarly, adult winter flounder constituting a brood stock were collected from Narragansett Bay, Rhode Island, and transferred to the laboratory. Flounder eggs were collected and fertilized using techniques described by Klein-MacPhee et al. (1982). Several egg clusters (n = 18) were measured for wet weight and dry weight (dried at 90 °C for >24 h) using a Mettler PM2000 digital scale (±0.001 g). The wet weight (W_W) – dry weight (W_D) relationship was derived from a least squares linear regression model with the intercept forced through the origin:

$$(1) \qquad W_D = 0.1101 W_W \qquad (R^2 = 0.998)$$

Feeding trials were conducted by placing nine glass chambers (13.5 cm × 17.5 cm × 14.0 cm) into a temperature-controlled water bath. Experimental chambers were part of a larger flow-through, recirculating system in which tempera-

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ture was maintained at desired levels by thermostatic control (±0.2 °C). Four temperatures were used in this experiment (2.0, 4.0, 6.0, and 10.0 °C), representing conditions experienced by the egg life stage of winter flounder in the field.

Before the onset of any feeding trials, shrimp and flounder eggs were acclimated to experimental conditions (temperature = 2–10 °C, light regime = 12 h light : 12 h dark) for 48 h. Shrimp were also starved 24 h prior to experiments to standardize hunger levels across treatments. After the specified acclimation period, individual shrimp measuring 34–62 mm total length (TL) from the tip of the antennal scale to the end of the telson were placed into a chamber containing fertilized flounder eggs (~4.0 g wet weight or 8810 eggs) that were 2–10 days postspawn. Fourteen to 24 replicate 48-h feeding experiments were conducted for each temperature treatment. At the conclusion of a feeding trial, the wet weight of eggs consumed by a shrimp was quantified by subtracting the weight of the remaining eggs in a chamber from the initial weight of eggs present at the start of the experiment. During each set of replicate trials, one chamber was left without a shrimp to serve as the control for changes in egg weight owing to factors other than predation. The change in egg weight during a control trial was then used to correct values of shrimp feeding rates. After this correction (average = ±0.01 g wet weight), the wet weight of eggs consumed was calculated as dry weight (eq. 1) and then converted to number of eggs eaten assuming that one flounder egg equals 50.0 µg dry weight (average dry weight for a 2- to 8-day postfertilized egg; Cetta and Capuzzo 1982). Results from feeding experiments were analyzed with a least squares multiple linear regression:

$$(2) \qquad F = \alpha + \beta_1 T + \beta_2 L + \beta_3 (T \cdot L)$$

where F is shrimp feeding rate (number of eggs eaten per shrimp per day), α is the intercept parameter, β_1 to β_3 are vectors of the slope parameters, T is water temperature (degrees Celsius), and L is shrimp TL (millimetres).

The volume of flounder eggs consumed by individual shrimp (V_E) (cubic centimetres) was analyzed relative to the stomach volume of shrimp (V_S) (cubic centimetres). Egg volume eaten was calculated as shrimp feeding rate (F) (eq. 2) divided by the spherical volume of a flounder egg with a diameter of 0.08 cm (Collette and Klein-MacPhee 2002). Predator stomach volume was calculated as a function of shrimp TL as reported for *Crangon crangon* (Gibson et al. 1995). Ratio of egg volume eaten to shrimp stomach volume was analyzed as a function of temperature (T) (degrees Celsius) and shrimp TL (L) (millimetres) with a least squares function:

$$(3) \qquad V_E : V_S = \alpha + \beta_1 T + \beta_2 L^{-3} + \beta_3 (T \cdot L^{-3})$$

Separate feeding trials were conducted to determine the effect of shrimp reproductive status on feeding rates of flounder eggs. The protocol for the second feeding experiment was the same as the previous, with the following exceptions. Experiments were run at 10.0 ± 0.2 °C, and only female shrimp measuring 46–61 mm TL were used in feeding trials. Shrimp were sexed by means of dimorphism observed on the endopodite of the first pleopod, and reproductive status (gravid female or nongravid female) was determined by the presence or absence of an egg mass attached to the abdomen (Price 1962). Fifteen replicate 48-h feeding experiments were conducted for each treatment. Again, during each set of replicate trials, one chamber was left without a shrimp to correct for changes in egg weight owing to factors other than predation. Weight of eggs consumed was converted to number of eggs eaten, and mean differences in shrimp feeding rates as a function of reproductive status were analyzed by a standard t test.

Shrimp stomach content analysis

Shrimp used for dietary analysis were collected by otter trawl during the adult winter flounder survey in the Niantic River (see below). Field sampling occurred from 18 February to 1 April 2002, and shrimp were collected in locations inhabited by gravid adult flounder (arm and basin) (Fig. 1). A random subsample of shrimp (n = 600) were immediately placed on ice after capture and then frozen at –20 °C on return to the laboratory. Bottom water temperature (degrees Celsius) was recorded at the time of shrimp collection.

Prior to dietary analysis, shrimp were thawed, TL was measured to the nearest millimetre, and reproductive and sexual status of the individual was determined as previously described (Price 1962). Qualitative immunoassays, utilizing the micro-Ouchterlony double-diffusion technique (Feller 1991), were used to analyze the stomach contents of shrimp for the presence or absence of winter flounder egg proteins. For a complete description of the experimental protocol and testing of the assay's sensitivity, specificity, and detection limits, refer to Taylor (2004). Briefly, two templates were placed on an agarose matrix, which in turn covered a microscope slide. Each template consisted of five wells, into which 20 µL of winter flounder egg specific antiserum was pipetted into a single central well. The remaining four additional wells surrounding and equidistant from the template's central well were loaded with 20 µL of antigen solutions prepared from solubilized stomach material from an individual shrimp (one stomach sample per well). Diffusion of antiserum and antigen solutions occurred within the agarose matrix, and precipitin lines formed between the central well and peripheral wells if antibodies within the antiserum reacted with antigenic moieties in the stomach content mixture. A positive reaction was defined as the formation of at least one distinct precipitin line, and the resulting reaction was confirmed with tests of identity (Taylor 2004).

Logistic regression analysis, employing the method of maximum likelihood, was used to test for a significant relationship between egg predation, sampling date, water temperature, shrimp body size, and shrimp reproductive and sexual status. The natural logarithm of the ratio of response frequencies (logits) was used to estimate parameters of a linear model. The proportion of shrimp stomachs containing flounder eggs (P) was given by

$$(4) \qquad \text{logit}(P) = \log\left(\frac{P}{1-P}\right) = \alpha + \beta_1 d + \beta_2 T + \beta_3 L + \beta_4 R$$

where α is the intercept parameter, β_1 to β_4 are vectors of the slope parameters, d is day of the year that shrimp were collected from the field (days 49–91), T is temperature (degrees Celsius), L is shrimp TL (22–65 mm), and R is shrimp

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reproductive and sexual status (nongravid female, gravid female, or male). Data were treated as frequency responses (presence or absence of eggs in shrimp stomachs) rather than continuous responses, and thus, a χ^2 value was calculated to test for significance of treatment variables.

Flounder egg production

Danila (2000) described the methods for sampling adult winter flounder in the Niantic River. Briefly, the 2002 winter flounder spawning survey began on 18 February and was completed on 1 April (days 49–91). Flounder were collected using a 9.1-m otter trawl with a 6.4-mm bar mesh codend liner. The survey was conducted as a stratified random design with tows performed in three separate sections of the estuary (arm, basin, and lower river) (Fig. 1). A total of 383 tows were made during the survey (n = 52–57 tows·week^{-1}), but sampling effort was concentrated in the arm and basin (83% of all tows) because of the greater abundance of reproductive flounder in these areas (Fig. 1). Most tows (92%) sampled a standardized distance of 0.55 km and tow times, which were affected by tidal currents and wind conditions, ranged between 10 and 20 min.

Flounder collected in trawls were measured for TL (centimetres), and gender and reproductive condition of larger individuals (>20 cm TL) were determined by either observing eggs or milt or noting the presence (males) or absence (females) of ctenii on the left-side caudal peduncle scales. Winter flounder reproductive season was determined by the rate of female spawning, which was estimated by observing weekly changes in the proportion of gravid fish larger than 26 cm, the size at which approximately one-half of all observed females were mature (Dominion Nuclear Connecticut, Inc. (DNC) 2003). To estimate the theoretical start and end of the spawning season (occurring before and after the observation period), we extrapolated the relative abundance of gravid flounder with a quadratic function to the day of the year when 100% and 0% of the females were bearing eggs, respectively. Accordingly, in the Niantic River, the 2002 spawning season was projected to start on 20 January (day 20) and conclude on 6 April (day 96) (Fig. 2*a*). The estimated spawning season in this study agrees with field and laboratory observations of winter flounder spawning habits (Stoner et al. 1999; Collette and Klein-MacPhee 2002).

Winter flounder egg density (number of eggs per square metre) over the 2002 spawning season was estimated daily by first subtracting the proportion of gravid females (G_d) on day d from 1.0 to calculate the proportion of females having spawned eggs (i.e., spent flounder = $S_d = 1.0 - G_d$) (Fig. 2*b*). A quadratic function was fit to the data by least squares analysis to estimate the proportion of spent females (S) as a function of day of the year (d), yielding the following equation (Fig. 2*b*):

$$(5) \qquad S = 1.21 \times 10^{-4} d^2 - 2.73 \times 10^{-2} d + 1.50 \qquad (R^2 = 0.866,\ n = 7)$$

Egg density on day d includes eggs spawned on that day plus eggs spawned earlier in the season that have yet to hatch. Flounder eggs were assumed to have an incubation period of 20 days based on average water temperature measured in the Niantic River during the field survey (Rogers 1976; DNC 2003). Egg density (E_p) was calculated daily from 20 January to 6 April 2002 (days 20–96) by the following equation (Fig. 2*b*):

$$(6) \qquad E_p = \frac{(S_d - S_{d-20})E_T}{A}$$

where S_d is the proportion of spent females on day d, S_{d-20} is the proportion of females having spawned eggs 20 days earlier, E_T is total egg production in the Niantic River in 2002 (3.14×10^9; DNC 2003), and A is total spawning area of the river. Danila (2000) provided a complete description for esti-

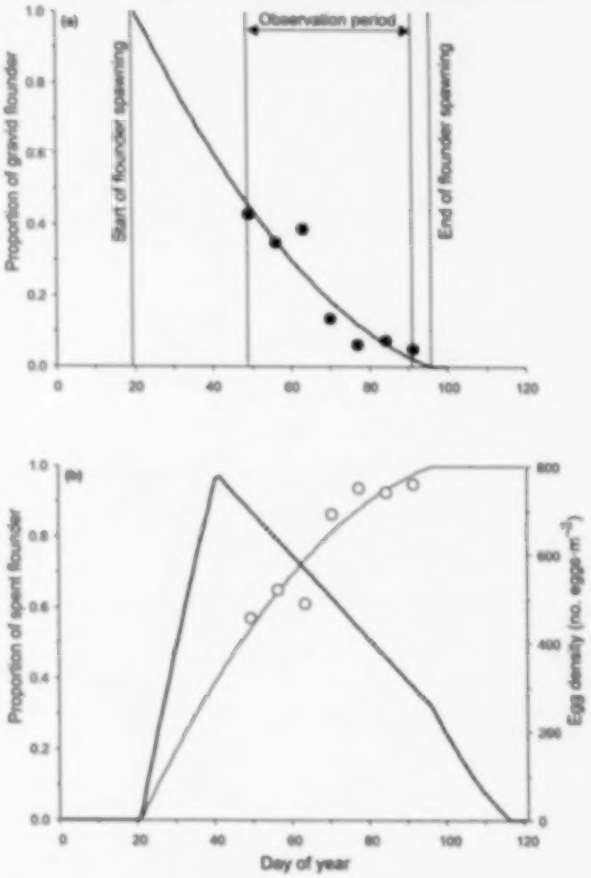

Fig. 2. (*a*) Proportion of gravid female winter flounder (*Pseudopleuronectes americanus*) (>26 cm TL) collected from the Niantic River, Connecticut, during the 2002 field survey (18 February to 1 April). The theoretical start and end of the flounder spawning season (occurring before and after the observation period) were determined by extrapolating the relative abundance of gravid flounder with a quadratic function to the day of the year when 100% and 0% of the females were bearing eggs, respectively. (*b*) Proportion of spent female winter flounder during the 2002 reproductive period (20 January to 6 April). Data points (circles) were fit with a quadratic function (thin line) to estimate the proportion of spent females as a function of day of the year. Predicted maximum density of flounder eggs throughout the spawning season is also presented (thick line).

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Table 1. Results of two model simulations predicting the number of winter flounder (*Pseudopleuronectes americanus*) eggs eaten during the spawning season (C_T) (number of eggs eaten·m^{-2}·season^{-1}) and cumulative egg mortality (M) (percentage of total eggs eaten) caused by sand shrimp (*Crangon septemspinosa*) predation.

	$\bar{\delta}$	$\bar{L}$	E_T	t_s	t_e	C_T (M) Mean	+1 SE	−1 SE
Simulation I								
Low shrimp density								
Small shrimp	1	15	3.14	20	76	149 (0.4)	535 (1.4)	52 (0.1)
Medium shrimp	1	30	3.14	20	76	898 (2.3)	1 304 (3.3)	625 (1.6)
Large shrimp	1	45	3.14	20	76	2 809 (7.2)	2 961 (7.6)	2 671 (6.8)
Moderate shrimp density								
Small shrimp	5	15	3.14	20	76	731 (1.9)	2 332 (5.9)	264 (0.7)
Medium shrimp	5	30	3.14	20	76	4 112 (10.5)	5 584 (14.2)	3 012 (7.7)
Large shrimp	5	45	3.14	20	76	11 707 (29.9)	12 109 (30.9)	11 336 (28.9)
High shrimp density								
Small shrimp	10	15	3.14	20	76	1 400 (3.6)	4 139 (10.6)	528 (1.3)
Medium shrimp	10	30	3.14	20	76	7 529 (19.2)	9 708 (24.8)	5 721 (14.6)
Large shrimp	10	45	3.14	20	76	19 499 (49.7)	20 092 (51.3)	18 951 (48.3)
Simulation II								
Low egg production								
Early spawning	5	30	2.68	−6	111	10 167 (28.9)	13 474 (38.3)	7 271 (20.7)
Average spawning	5	30	2.68	6	100	6 966 (20.5)	9 450 (27.8)	4 943 (14.5)
Late spawning	5	30	2.68	13	106	5 261 (16.5)	7 158 (22.4)	3 731 (11.7)
Moderate egg production								
Early spawning	5	30	13.9	−6	111	13 182 (7.2)	20 169 (11.1)	8 641 (4.7)
Average spawning	5	30	13.9	6	100	8 428 (4.8)	12 721 (7.2)	5 563 (3.2)
Late spawning	5	30	13.9	13	106	6 016 (3.6)	8 963 (5.4)	4 054 (2.5)
High egg production								
Early spawning	5	30	25.1	−6	111	13 609 (4.1)	21 283 (6.5)	8 795 (2.7)
Average spawning	5	30	25.1	6	100	8 628 (2.7)	13 264 (4.2)	5 628 (1.8)
Late spawning	5	30	25.1	13	106	6 133 (2.1)	9 237 (3.1)	4 066 (1.4)

Note: Simulation I varied conditions of shrimp density ($\bar{\delta}$) (total number of shrimp·m^{-2}) and shrimp mean body size ($\bar{L}$) (mm TL). Simulation II varied conditions of total flounder egg production (E_T) (billions), start date of flounder spawning season (t_s) (day of the year), and duration of flounder spawning season (t_e) (days). Estimates of egg mortality were calculated as ranges by running the deterministic model with initial parameter estimates of shrimp feeding rates (mean ± 1 SE of the parameter estimates (eq. 2; Table 2).

mating total egg production of winter flounder in the Niantic River. The area of the Niantic River used by flounder for spawning ($A = 8.7 \times 10^5$ m^2) was approximated from the total area of the river (3.2×10^6 m^2) and scaled according to the spatial distribution of reproductive females and males observed during field surveys (DNC 2003) (Fig. 1). Examination of the length–frequency distribution of gravid and spawned females indicates that there were no size-related differences in the timing of spawning, with the exception of the very largest individuals (>45 cm) that completed spawning earlier in the season (Buckley et al. 1991*b*; DNC 2003). Because large flounder constitute a small portion of the adult population (1977–2002: range = 0.0%–4.6%, mean = 1.5%), their contribution to size-dependent effects on temporal spawning was negligible.

Modeling flounder egg mortality

Mortality of winter flounder eggs owing to shrimp predation was assessed with a deterministic model (Table 1). The model tracked the spawning and mortality of flounder eggs in the Niantic River during a defined reproductive season. The number of flounder eggs eaten by the shrimp population was calculated by summing the daily consumption rate of shrimp (C_d) (number of eggs eaten per square metre per day), individually defined by length L (millimetres TL):

$$(7) \qquad C_d = \sum \frac{F_L P_L \delta_L}{l_L}$$

where F is feeding rate (number of eggs eaten per shrimp per day) (eq. 2), δ is shrimp density (number of shrimp per square metre), P is the proportion of field-collected shrimp whose stomach contents tested positive for flounder eggs (eq. 4), and l is the time limit (days) for detecting egg proteins in the stomach contents of shrimp (range = 0.47–0.93 days for 10- to 70-mm TL shrimp; Taylor 2004). The number of eggs consumed on a daily basis could not exceed the number of available eggs on day d (Fig. 2*b*).

Temperature data incorporated into eq. 2 were obtained from continuous recorders at the intakes of the Millstone Power Station located on Niantic Bay (Waterford, Connecticut; Fig. 1) (DNC 2003). To ensure that Niantic Bay temperatures accurately reflected those in the Niantic River, we analyzed differences in temperature between locations (river and bay) by an analysis of covariance model with day of the year (days 49–91) as the covariate and location as the dis-

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crete explanatory variable. Temperature was positively correlated with day of the year (F = 43.63, df = 1,53, p < 0.0001), irrespective of location. Moreover, there was no difference in temperature between locations (F = 2.01, df = 1,53, p = 0.162), and the interaction effect between day of the year and location was not significant (F = 2.27, df = 1,53, p = 0.138).

Population density and size structure of shrimp (δ_L) in the Niantic River was not explicitly examined in this study. To account for this uncertainty, we used several model runs over a range of potential shrimp density and size structure values (simulation I, Table 1). The size frequency of shrimp was modeled as a normal distribution (SD ±10 mm). In simulation I, nine model runs accounted for variability in shrimp mean TL ($\bar{L}$ = 15, 30, and 45 mm TL) and population density (δ = 1, 5, and 10 shrimp·m^{-2}). The defined size structure and density of shrimp were set for day 1 in the model. Each following day, shrimp experienced a natural mortality rate of 0.01·day^{-1} (Modlin 1980; Oh et al. 1999) and a growth rate expressed as (modified from Wilcox and Jeffries 1973):

$$(8) \qquad g = 8.86\times10^{-3}\,T - 1.20\times10^{-3}\,L + 3.29\times10^{-2}$$

where g is daily increase in shrimp TL (millimetres per day) and the remaining parameters are defined above.

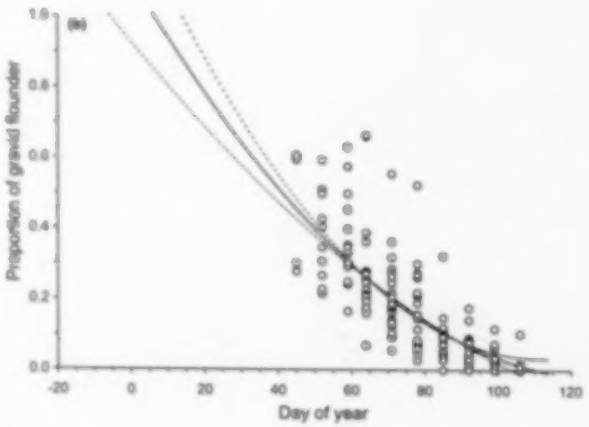
Total number of eggs eaten during the spawning season (C_T) (number of eggs eaten per square metre per season) was calculated by summing daily consumption rates over the estimated reproductive period and 20 days beyond (days 20–116):

$$(9) \qquad C_T = \sum_{d=20}^{116} C_d$$

Total egg mortality (M) caused by shrimp predation was estimated by dividing the total number of eggs consumed during the spawning season (C_T) by total egg production in 2002.

A second model simulation (simulation II) accounted for annual variations in winter flounder egg production and temporal dynamics in the spawning season, i.e., start date (t_i) (day of the year) and duration (t_t) (days) (Table 1; Fig. 3). In the Niantic River, the average (±SD) annual egg production of flounder between 1977 and 2002 was 13.9 (±11.2) × 10^9 eggs (DNC 2003) (Fig. 3*a*). Moreover, the theoretical start and end of the flounder spawning season were calculated as previously described (see Flounder egg production), with the following exceptions. Observations combined data from 1977 to 2002, and multiple quadratic functions were fit to the data (mean ± 1 SE of parameter estimates) (Fig. 3*b*). Based on these quadratic functions, three unique spawning seasons were recreated: (*i*) early spawning (27 December, day –6) lasting 111 days, (*ii*) mean spawning (6 January, day 6) lasting 106 days, and (*iii*) late spawning (13 January, day 13) lasting 100 days. In simulation II, nine model runs accounted for variability in flounder egg production (E_T = 2.68, 13.9, and 25.1 × 10^9 eggs) and temporal dynamics in spawning season (t_i = –6, 6, and 13 day of the year; t_t = 111, 106, and 100 days, respectively). In simulation II, shrimp had an initial mean size ($\bar{L}$) of 30 mm TL and a total population density (δ) of 5 shrimp·m^{-2} and C_T and M were estimated as previously described.

Fig. 3. (*a*) Winter flounder (*Pseudopleuronectes americanus*) egg production in the Niantic River, Connecticut. (*b*) Proportion of gravid winter flounder during the reproductive period (1977–2002). Data points (circles) were fit with multiple quadratic functions (solid line, mean of parameter estimates; broken lines, ±1 SE of parameter estimates) to estimate the temporal dynamics of the flounder spawning season (i.e., start and end date and duration of season).



For simulations I and II, C_T and M were calculated as ranges by evaluating the model with shrimp feeding rates (F) (eq. 2) equal to the mean ± 1 SE of predicted parameter estimates (Table 2).

Flounder density-dependent egg mortality

Density-dependent mortality between the egg and yolk-sac larval life stage was examined for the winter flounder population in the Niantic River from 1984 to 2002. Annual egg and larval abundance estimates are provided in DNC (2003). Presence of density-dependent mortality between successive life stages was examined with a linear Ricker stock–recruitment model and testing for a significant correlation between survival rate (i.e., difference in the natural

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Table 2. Sand shrimp (*Crangon septemspinosa*) temperature- and size-dependent feeding rate on winter flounder (*Pseudopleuronectes americanus*) eggs (number of eggs eaten·shrimp^{-1}·day^{-1}) and the ratio between egg volume eaten (cm^3) and shrimp stomach volume (cm^3).

Variable	Parameter estimate	SE	p
Feeding rate			
Intercept	533.24	477.45	0.268
Temperature	−202.3	63.23	<0.005
Size	−11.38	9.45	0.233
Temperature × size	5.87	1.28	<0.001
Egg volume : stomach volume			
Intercept	−0.917	0.593	0.126
Temperature	0.451	0.083	<0.001
Size^{-1}	102 300	64 276	0.116
Temperature × size^{-1}	−13 028	8 000	0.108

logarithm of abundance between the larval and egg life stage) and flounder egg abundance:

$$(10) \quad \ln\left(\frac{N_L}{N_E}\right) = \ln(a) + bN_E$$

where N_L and N_E are the abundance of yolk-sac larvae and eggs, respectively, a is the productivity parameter (or density-independent survival rate), and parameter b measures the level of density dependence. Constants (a and b) were estimated by the method of least squares linear regression analysis. A nonsignificant value for the density-dependent parameter (i.e., $b = 0$) is indicative of density-independent mortality. Conversely, a significantly negative b denotes compensatory density-dependent mortality, whereas a significantly positive b indicates depensation.

Density-dependent mortality between the egg and larval life stage was analyzed by combining annual abundance estimates across years in addition to grouping data according to annual spawning water temperature averaged from January to April (cold year <4.3 °C, warm year ≥4.3 °C). The separation point (4.3 °C) was chosen because it represents the median spawning water temperature over the data time series. Effects of egg abundance on flounder survival rate (i.e., differences in the estimates of a and b from the Ricker model) as a function of spawning temperature (cold or warm year) were analyzed with the Fisher–Behrens statistic, where variances need not be constant across treatments and the statistic is compared with a critical value of a t distribution (Cerrato 1990).

Results

Laboratory feeding experiments

Shrimp feeding rates on flounder eggs (F) (number of eggs eaten per shrimp per day) differed significantly by temperature but not by predator size (Table 2; Figs. 4*a* and 4*b*). The interaction effect between temperature and shrimp body size was significant, however, precluding contrasts across the main effects. The interaction effect was attributed to shrimp body size having a more pronounced impact on feeding rates at warmer temperatures. Similarly, temperature effects on the number of eggs consumed were maximal at larger shrimp sizes.

The volume of flounder eggs consumed (V_E) (cubic centimetres) relative to the shrimp's stomach volume (V_S) (cubic centimetres) differed significantly by temperature but not by shrimp TL (Table 2; Figs. 4*c* and 4*d*). The interaction effect was not significant. Averaged across shrimp body size, the ratio between V_E and V_S was approximately 0.58 at 2 °C. Increasing temperature to 10 °C resulted in a significant 5.7-fold increase in V_E:V_S. Shrimp foraging on flounder eggs at cold temperatures did not feed to satiation, whereas at warmer temperatures, shrimp consumed enough eggs to fill their stomach volume approximately three times over a 24-h period.

Gravid shrimp tended to consume fewer flounder eggs relative to non-egg-bearing females of the same size (789 and 956 eggs consumed for gravid and nongravid shrimp, respectively). These differences were not significant (standard t test: $t = 1.623$, df = 1,28, $p = 0.116$), however, and shrimp reproductive status was determined to have no effect on feeding rates.

Shrimp stomach content analysis

Six hundred shrimp were collected from winter flounder spawning sites (February to April), of which 43 (7.2%) of the stomachs examined tested positive for flounder eggs. Incidence of eggs in shrimp stomachs (averaged over all predator sizes) was greatest in mid-February (20.0%) and significantly decreased at a decelerating rate to 1.2% by early April (Table 3; Fig. 5*a*). Temporal trends in the proportion of shrimp stomachs containing eggs corresponded to a decrease in gravid female flounder collected during the observation period and consequently the estimated seasonal egg density (Fig. 2). Proportion of shrimp stomachs containing flounder eggs was statistically independent of temperature. Similarly, predator body size was not significant, owing in large part to low sample sizes for small and large shrimp. The predicted model, however, suggests that the likelihood of a predation event increases with increasing shrimp size, particularly early in the flounder spawning season. Shrimp reproductive and sexual status (female, gravid female, or male) was not a significant factor in the proportion of predator stomachs testing positive for flounder eggs (Table 3), hence corroborating results from laboratory feeding experiments.

Modeling flounder egg mortality

In simulations I and II, estimated mean daily consumption rate of shrimp (C_d) ranged between 0 and 594 eggs eaten·m^{-2}·day^{-1} (Fig. 6). Summing the number of eggs eaten daily over the entire flounder spawning season resulted in a total consumption rate (C_T) of 149 – 19 499 eggs eaten·m^{-2}·season^{-1} (average of simulations I and II (mean) = 7068 eggs eaten·m^{-2}·season^{-1}) (Table 1). Cumulative mortality of flounder eggs (M) resulting from shrimp predation ranged between 0.4% and 49.7% (average of simulations I and II (mean) = 12.0%) (Table 1).

Variations in shrimp population size structure and abundance (simulation I) accounted for the greatest variability in egg mortality (Table 1; Figs. 6*a*–6*c*). For example, flounder

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Fig. 4. (*a*) Observed and (*b*) predicted sand shrimp (*Crangon septemspinosa*) feeding rate on winter flounder (*Pseudopleuronectes americanus*) eggs as a function of water temperature and shrimp size ($R^2 = 0.672$, $F = 50.48$, df = 3,74, $p < 0.001$) and (*c*) observed and (*d*) predicted ratio between flounder egg volume eaten (cm^3) and shrimp stomach volume (cm^3) as a function of water temperature and shrimp size ($R^2 = 0.572$, $F = 32.90$, df = 3,74, $p < 0.001$).

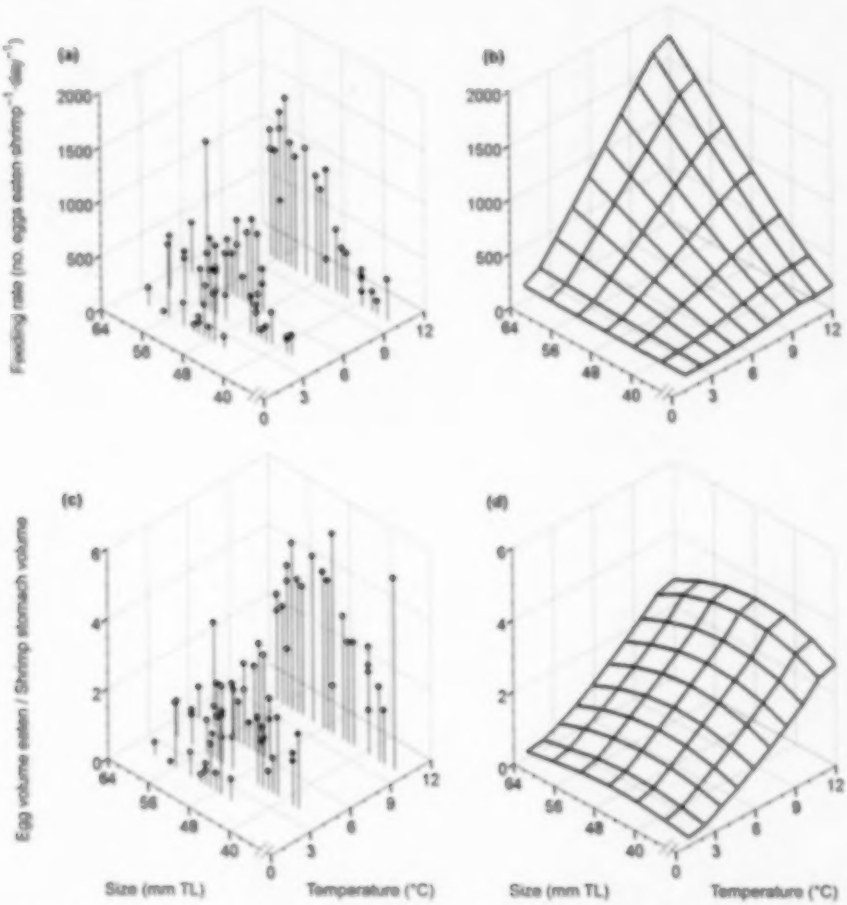

Table 3. Proportion of sand shrimp (*Crangon septemspinosa*) stomachs containing winter flounder (*Pseudopleuronectes americanus*) eggs as a function of sampling date (day of the year), bottom water temperature (°C), shrimp body size (mm TL), and shrimp reproductive and sexual status (nongravid female, gravid female, male).

Variable	Parameter estimate	SE	χ^2	p
Intercept	-0.98	1.518	0.42	0.518
Sampling date	-0.076	0.03	6.65	<0.01
Temperature	0.315	0.283	1.24	0.265
Size	0.036	0.03	1.44	0.23
Reproductive status	0.011	0.27	0.07	0.788

Note: Proportions are the natural logarithm of the ratio of response frequencies (logits): $\text{logit}(P) = \log[P/(1 - P)]$.

eggs suffered a 94% increase in mortality when the mean body size of shrimp ($\bar{L}$) increased from 15 to 45 mm TL. Similarly, increasing shrimp density from 1 to 10 shrimp·m^{-2} caused flounder eggs to experience an 88% increase in mortality.

Annual variations in winter flounder egg production and temporal dynamics in the spawning season affected estimates of egg mortality (simulation II), albeit not to the extent predicted with changes in shrimp population dynamics (Table 1; Figs. 6*d*–6*f*). In years of low egg production, flounder eggs experienced a 14%–25% increase in mortality relative to years when production was high. When the flounder spawning season started early in the year and was long in duration, eggs suffered a 48%–55% increase in mortality relative to instances when the reproductive period was relatively late in the year and short in duration.

Flounder density-dependent egg mortality

The Ricker stock–recruitment model fit to flounder egg and yolk-sac larval abundance indicated that in years of cold spawning temperature, larval numbers generally increased monotonically with increasing egg density (Fig. 7*a*). Conversely, in warm years, larval numbers reached an asymptote

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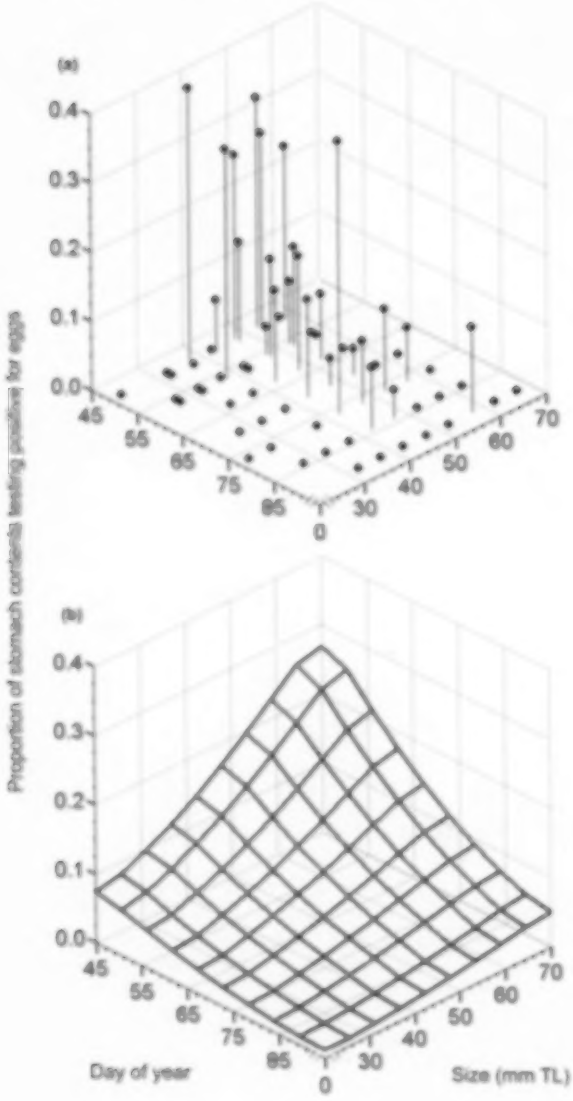
Fig. 5. (*a*) Proportion of sand shrimp (*Crangon septemspinosa*) stomach contents testing positive for winter flounder (*Pseudopleuronectes americanus*) eggs as a function of day of the year and shrimp size. Shrimp (n = 600) were collected from the Niantic River, Connecticut, between 18 February and 1 April 2002. Data points were pooled for shrimp at 4-mm intervals for graphic representation only. (*b*) Proportion of shrimp stomachs containing flounder eggs predicted from logistic regression analysis.



at moderate egg densities and were depressed considerably at high egg densities, indicating stronger effects of compensatory processes that increased egg mortality and limited the abundance of yolk-sac larvae. Density-dependent mortality between the egg and larval life stage was examined statistically by testing for a significant correlation between survival rate and flounder egg abundance (Fig. 7*b*). There was a nearly significant negative correlation (b = –0.062) between survival rate and egg abundance when data were analyzed across all years (R^2 = 0.198, F = 4.20, df = 1,17, p = 0.056), indicating the possibility of compensatory density-dependent mortality. There was strong evidence of compensatory density-dependent mortality in years when the average spawning water temperature was ≥4.3 °C (R^2 = 0.954, F = 145.54, df = 1,7, p < 0.001). Conversely, egg survival was independent of density when flounder spawned in cold-water conditions (R^2 = 0.026, F = 0.214, df = 1,8, p = 0.656). The slope of the regression between survival rate and egg abundance was more negative when flounder spawned during warm years relative to cold years (Fisher-Behrens test: z = 2.368, df = 2,15, p < 0.05), suggesting an increase in compensatory mortality when the average spawning water temperature exceeded 4.3 °C. The difference in estimates of a between warm and cold years was not significant (Fisher-Behrens test: z = 1.863, df = 2,15, p = 0.082).

Discussion

Winter flounder have historically supported one of the most valuable commercial and recreational fisheries along the northeastern United States. The New England – mid-Atlantic stock complex, in particular, has been heavily exploited in the recent past, consequently decreasing flounder abundance to record low levels (Northeast Fisheries Science Center 2003). Despite management efforts to reduce further stock losses owing to fishing mortality, discrete subpopulations of winter flounder continue to decrease for reasons that are unknown. Although overexploitation was paramount in the initial population decline, several other factors could continue to adversely affect flounder recruitment and keep adult populations at depressed levels. The precipitous decline in flounder abundance, for example, coincides with a significant warming trend in many northwest Atlantic estuaries (Keller and Klein-MacPhee 2000; DNC 2003). Moreover, flounder recruitment is negatively correlated with winter temperature (Jeffries and Terceiro 1985; Keller and Klein-MacPhee 2000; DNC 2003). Jeffries and Terceiro (1985) proposed that climate-induced effects on the trophic system dictate the survival rate of early-stage winter flounder in Narragansett Bay, Rhode Island. Keller and Klein-MacPhee (2000) determined that warm winter temperatures resulted in a 10%–16% reduction in the survival of flounder to metamorphosis owing to increased predatory losses. The purpose of this study was to identify the importance of sand shrimp as a predator of winter flounder eggs and assess the implications of increasing winter temperature on predator–prey dynamics and the regulation of flounder year-class strength and recruitment. Research that quantifies the impact of predation during the early life history of winter flounder is crucial to our understanding of whether these stocks can recover from previous overexploitation.

Elevated water temperatures resulted in a significant increase in shrimp feeding rates on winter flounder eggs. Several investigators proposed that increased temperature intensifies predator-induced mortality on the early life stages of flatfish by increasing the metabolism and subsequently the consumption rate of potential benthic predators (Van der

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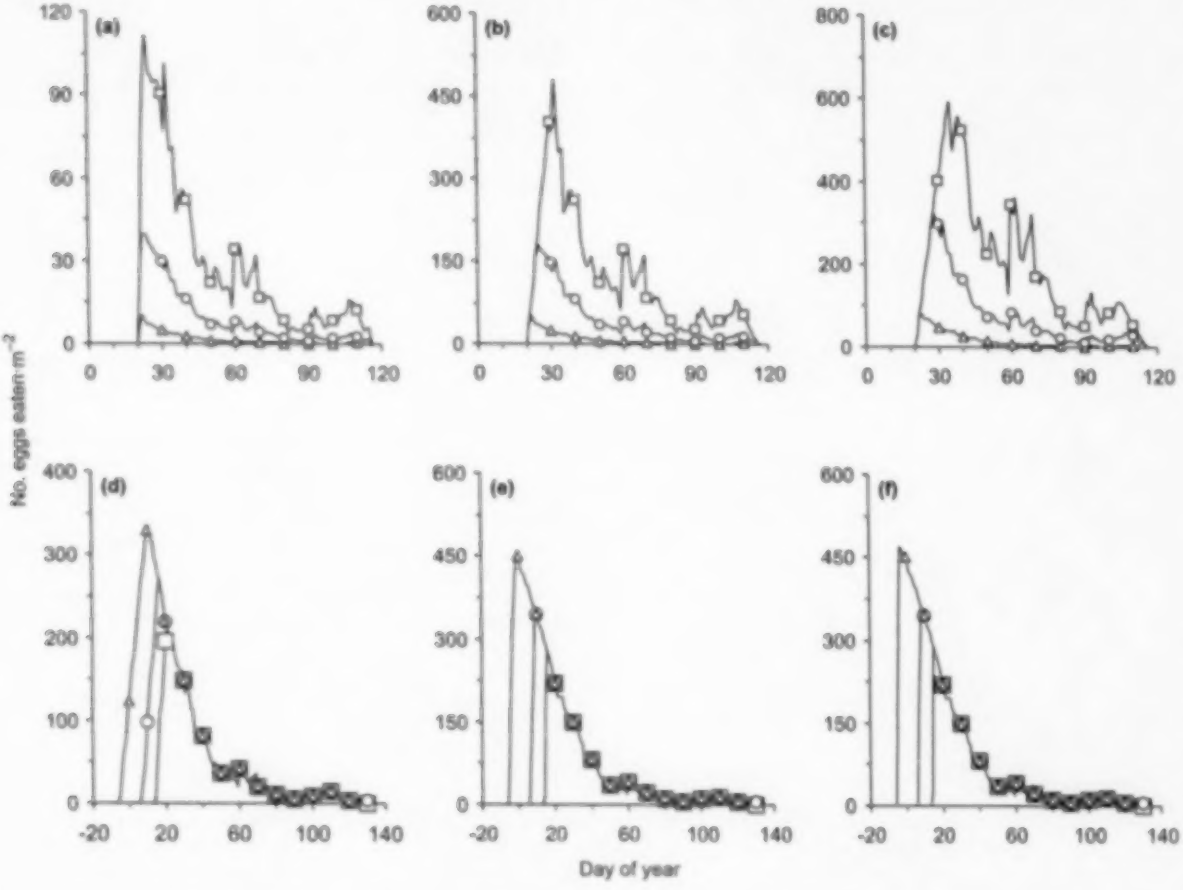
Fig. 6. Model simulations estimating sand shrimp (*Crangon septemspinosa*) consumption rates of winter flounder (*Pseudopleuronectes americanus*) eggs. (*a–c*) Simulation I varied conditions of shrimp density ($\bar{\delta}$) ((*a*) low shrimp density (1 shrimp·m^{-2}), (*b*) moderate shrimp density (5 shrimp·m^{-2}), and (*c*) high shrimp density (10 shrimp·m^{-2})) and shrimp mean body size ($\bar{L}$) (triangles, small shrimp (15 mm TL); circles, medium shrimp (30 mm TL); squares, large shrimp (45 mm TL)). (*d–f*) Simulation II varied conditions of total egg production (E_T) ((*d*) low egg production (2.68 × 10^9 eggs), (*e*) moderate egg production (13.9 × 10^9 eggs), and (*f*) high egg production (25.1 × 10^9 eggs)) and temporal dynamics of the spawning season (t_i and t_s) (triangles, early spawning (27 December, day –6) lasting 111 days; circles, mean spawning (6 January, day 6) lasting 106 days; squares, late spawning (13 January, day 13) lasting 100 days).



Veer et al. 1990; Keller and Klein-MacPhee 2000). Temperature is a critical determinant of the metabolic rate of sand shrimp (Taylor and Peck 2004). Accordingly, the acceleration of shrimp metabolism at warmer temperatures is likely to increase predation intensity on flounder eggs because of predators compensating for greater energy requirements. Moreover, the daily foraging effort of shrimp exposed to cold temperatures (2 °C) was below the individual's projected satiation level, whereas at higher temperatures (10 °C), shrimp consumed enough eggs to fill their stomach volume approximately three times over a 24-h period. Sand shrimp require 6–12 h after feeding to empty the cardiac portion of their stomach (Wilcox and Jeffries 1974); hence, shrimp feeding rates and satiation levels estimated in this study are feasible.

Quantifying predatory impacts on the early life history of fish has been a formidable challenge in fisheries research because of difficulties in visually identifying the remnants of soft-bodied prey, such as fish eggs, in the stomachs of suspected predators. The immunological assay described in this study offers an alternative approach to visual estimations by providing a means of positively identifying flounder egg proteins in the stomach contents of shrimp. Accordingly, immunoassays successfully identified sand shrimp as predators of winter flounder eggs in natural populations. The presence of flounder eggs in shrimp stomach samples suggested a temporal trend of decreasing predation pressure throughout the field survey in the Niantic River. This trend initially appears counterintuitive considering that later in the season, temperatures are warmer and the expectation is that shrimp feeding rates are enhanced. However, warmer temperatures also increase the digestion rate of shrimp and the clearance of eggs from the stomach, thus making it more difficult to detect a predation event with the immunoassay (Taylor 2004).

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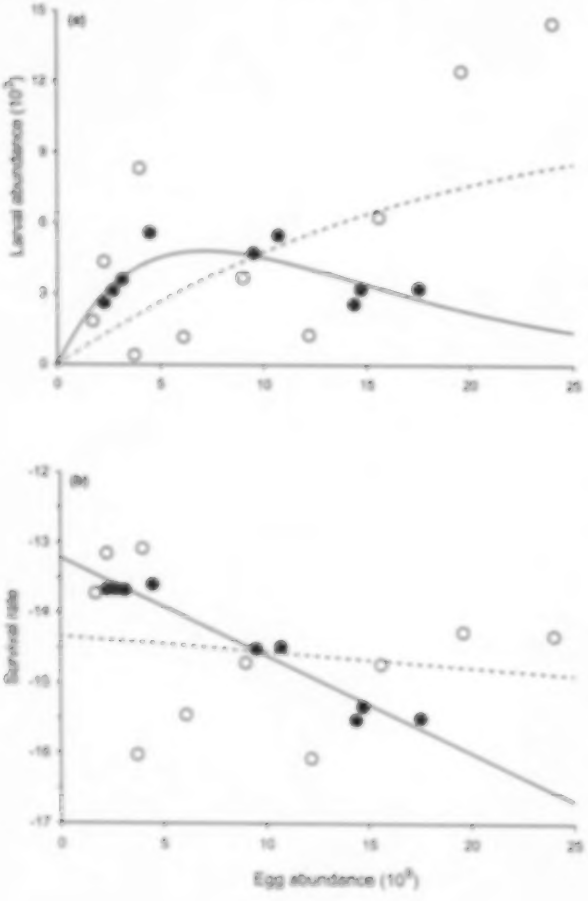
Fig. 7. (*a*) Comparison between annual abundance of the egg and larval life stage of winter flounder (*Pseudopleuronectes americanus*) in the Niantic River, Connecticut. Egg and larval abundance data were grouped according to annual spawning water temperature averaged from January to April 2002. Cold (<4.3 °C) and warm (≥4.3 °C) years are represented by open and solid circles, respectively. (*b*) Richer stock–recruitment models were also fit to the data (broken line, cold; solid line, warm), and model parameters were estimated from the linear regression of survival rate (i.e., difference in the natural logarithm of abundance between the larval and egg life stage) and flounder egg abundance. Cold year: $\ln(N_L/N_E) = \ln(5.95 \times 10^{-7}) - 0.022N_E$ ($R^2 = 0.026$); warm year: $\ln(N_L/N_E) = \ln(1.82 \times 10^{-6}) - 0.139N_E$ ($R^2 = 0.954$).



The observed temporal trend in egg predation also involves the timing of winter flounder spawning. The incidence of eggs in shrimp stomachs, for example, was maximal in mid-February at the height of the winter flounder spawning period. Predation on flounder eggs then decreased significantly over time, reflecting the end of the spawning season and the relatively low abundance of eggs during early spring.

This investigation identified sand shrimp as a potentially important predator of winter flounder eggs, capable of consuming 0.4%–49.7% (average across model simulations = 12.0%) of the total flounder spawn in the Niantic River. This estimate is assumed to be a maximal rate, however. Foremost, shrimp whose stomachs contents tested positive for flounder eggs were assumed to feed at rates determined from laboratory experiments. This is likely to be an overestimate considering that shrimp were provided unlimited food resources, as egg densities in experimental chambers far exceeded natural levels (3.6×10^3 eggs·m^{-2}) (De Lafontaine and Leggett 1987). Moreover, the prey search component of the predation process was dramatically reduced for shrimp under laboratory conditions because of the inflated egg densities and constraints imposed by chamber size. Immunological assays may also overestimate predation rates by incorrectly asserting that shrimp have ingested flounder eggs, or a false-positive result. This is frequently caused by nonspecific antiserum that cross-reacts with heterologous antigens from the predator or nontarget prey (see Taylor (2004) for antiserum quality control). Other fish species inhabiting the Niantic River and spawning demersal eggs during the winter include the Atlantic tomcod (*Microgadus tomcod*), American sand lance (*Ammodytes americanus*), grubby (*Myoxocephalus aenaeus*), and rock gunnel (*Pholis gunnellus*). However, the first two species were infrequently found in the river during recent years and the rock gunnel typically exhibits parental care and nest defense (Collette and Klein-MacPhee 2002). Moreover, flounder egg antiserum used in this study does not cross-react with heterologous antigens created from sculpin tissue (Taylor 2004). False-positive results from immunoassays may also be caused by circumstantial limitations and not methodological problems with antisera, such as predation in nets during field sampling, and secondary detection, i.e., stomach contents of shrimp contain prey whose stomach contents contain flounder eggs (Feller 1992; Taylor 2004). Finally, temperature data incorporated into model simulations were from 2002. The average winter water temperature in the Niantic River in 2002 (January through March = 5.67 °C) was the highest recorded since observations began in 1976 (overall mean = 3.80 °C) (DNC 2003). Thus, if shrimp predation on flounder eggs is partially governed by water temperature, egg mortality rates estimated from model simulations are expected to be greater relative to cooler years. One plausible mechanism that could reduce cumulative mortality in a warm year is increased temperatures thermally accelerating egg development rates, which in turn minimizes the duration that eggs are susceptible to oophagous predators (Rogers 1976). However, the simultaneous influence of increased temperature on the predator's metabolic demand, and thus foraging rate, precludes the advantages of a shortened incubation period (i.e., temporal refuge is inadequate relative to increased predation pressure) (Rajasilta et al. 1993; Keller and Klein-MacPhee 2000).

Water temperature during the spawning period is an important factor underlying the population dynamics of the early life history stages of winter flounder. Cold spawning temperatures resulted in the density-independent mortality of flounder, as yolk-sac larvae numbers generally increased monotonically with increasing egg density. Conversely, in warm years, larval numbers reached an asymptote at moderate egg densities and were depressed considerably at high egg densities, indicating strong compensatory processes that

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increased egg mortality and limited the abundance of yolk-sac larvae. This trend of increased mortality at high egg densities during warm years is not exclusive to the Niantic River. Depressed winter flounder populations in several other northern-temperate estuaries are currently experiencing density-dependent mortality of the egg life stage, including populations in Long Island Sound, Narragansett Bay, Mount Hope Bay (Rhode Island – Massachusetts), and southern Massachusetts (Collie and DeLong 2002). The failure of winter flounder to produce strong year-classes of larvae during recent warm years may explain the inability of stocks to recover to historical levels in these geographic regions.

The effect of temperature on the annual survival rate of winter flounder eggs is possibly related to the additional effect of temperature on the physiology and behavior of potential predators, such as sand shrimp. First, increased water temperature directly influences the physiology of shrimp by enhancing metabolic activity, thus increasing their feeding rates on flounder eggs (Taylor and Peck 2004; this study). Second, the warming trend experienced in northern-temperate estuaries may result in shrimp foregoing seasonal offshore migrations, which in turn causes a spatial and temporal overlap with the estuarine spawning of winter flounder eggs (Jeffries and Johnson 1974; Boddeke 1976; Temming and Damm 2002). Similarly, winter water temperature indirectly influences plaice (*Pleuronectes platessa*) recruitment by affecting the spatial distribution and overall survival of overwintering *C. crangon* populations (Van der Veer et al. 1990, 2000). Plaice have highly successful recruitment classes following cold winters because of a reduction or absence of *C. crangon* predators, i.e., decreasing temperatures minimize shrimp numbers by inducing extensive mortality or forcing shrimp to migrate to deeper water (Van der Veer et al. 2000). Consequently, warm water conditions are expected to maximize epibenthic predation and alter predator–prey dynamics in such a way that the mortality of early-stage flatfish is compensatory.

The compensatory density-dependent mortality of flounder eggs during warm years may be caused by the combined effect of a numerical and a functional response of predatory sand shrimp to fluctuations in annual egg density (Solomon 1949; Holling 1959). Shrimp possibly exhibit a numerical response by congregating in areas of high egg density (i.e., aggregative response) and leaving those egg patches when the rate of prey consumption falls below a threshold necessary to sustain constant foraging efforts (Taylor and Collie 2003). Shrimp may also demonstrate a functional response whereby predator efficiency in the detection of flounder eggs decreases at low egg densities because there are insufficient chemical cues for shrimp to locate egg patches (Taylor and Collie 2003). For the feeding behavior of shrimp, olfactory chemical stimuli play a key role in mediating the various stages of feeding, including initial excitation, prey location, and sustained foraging (Wilcox and Jeffries 1974; Pittet et al. 1996). As a consequence of both the numerical response and functional response, predator-induced mortality of flounder eggs decreases at low egg densities because of a reduction in shrimp foraging activity in unrewarding circumstances (Taylor and Collie 2003) or shrimp switching to alternative sources of food when flounder eggs are scarce (Wennhage 2002).

Elevated temperatures in winter flounder spawning areas can adversely affect the survival of early-stage fish by means other than epibenthic predation. In a series of mesocosm experiments, Keller and Klein-MacPhee (2000) determined that the percent hatch of flounder eggs was significantly lower in systems maintained at warm temperatures (average = 5.11 °C) relative to cold temperatures (average = 1.86 °C), whereby the percent hatch for warm and cold treatments ranged from 64.6% to 81.8% and from 91.3% to 94.0%, respectively. Moreover, the size of larvae at hatching in systems maintained at cold temperatures was significantly larger than the size of fish exposed to warm temperatures (3.2 and 3.0 mm standard length for cold and warm treatments, respectively) (Keller and Klein-MacPhee 2000). Buckley et al. (1990) also noted that the spawning and incubation of winter flounder eggs in cold temperatures (2 °C) resulted in larvae that were significantly larger at hatching and in better condition (i.e., high RNA and protein content) relative to individuals reared in warm temperatures (7 °C). Increased size-at-age may have important consequences on the survival of flounder larvae because larger fish generally have greater escape swimming speeds, responsiveness to predatory attacks, and prey capture success (Miller et al. 1988; Blaxter and Fuiman 1990; Williams and Brown 1992). However, the water temperatures experienced in northern-temperate estuaries during the flounder reproductive period remain within the physiological tolerances of the fish (Rogers 1976; Buckley et al. 1990), suggesting that the negative effect of temperature on winter flounder abundance is mediated by predator–prey relationships (Jeffries and Terceiro 1985).

This investigation determined that sand shrimp predation on winter flounder eggs is a key mortality factor with possible important consequences on fish year-class strength. Crangonid shrimp were the emphasis of this study because of their recognized numerical dominance in estuarine and coastal areas (Price 1962; Modlin 1980). Yet other potential predators, e.g., green crab (*Carcinus maenas*), sculpin (*Myoxocephalus* spp.), skate (*Raja* spp.), and hake (*Urophycis* spp.) (Frank and Leggett 1984 and references therein), could contribute to the cumulative mortality of the flounder egg stage. Hence, predator-induced mortality during embryonic development is perhaps the most significant factor regulating the population size of demersal spawners (Frank and Leggett 1984). Moreover, climate-induced changes in trophic interactions may be critical in regulating the survival of early-stage flounder. The cumulative effect of the warming trend in many northwest Atlantic regions adversely affects egg survival, possibly as a result of intensified crangonid shrimp predation. Thus, the recent increases in winter temperatures may explain the failure of winter flounder stocks to recover to historical levels.

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Estimation of change in lifetime egg production from length frequency data

Michael R. O'Farrell and Louis W. Botsford

Abstract: The percentage of unfished lifetime egg production (LEP) has been used to represent persistence in precautionary fisheries management, but estimation of this reference point requires substantial data and it is sensitive to errors in natural mortality rate. We present an estimation method that quantifies the change in LEP by a fishery when only length frequency samples, one early in the fishery and one recent, are available for assessment. Using simulated length frequency data with known parameter values, estimates of LEP had undetectable bias when challenged with random sampling variability and sample sizes as low as 100. Simulation of artificial data with (*i*) growth parameters that differed from the estimation model, (*ii*) transient size structures, and (*iii*) recruitment variability led to predictably biased estimates. In a direct comparison with the spawning potential ratio reference point, fractional LEP was much less sensitive to errors in natural mortality rate. Application of this method to length frequency data for blue rockfish (*Sebastes mystinus*) for years between 1980 and 2003 suggests that during this interval, LEP has been reduced to levels of concern.

Résumé : Le pourcentage de la production d'oeufs au cours de la vie (LEP) qui n'est pas récolté sert en gestion prudente de la pêche de mesure de la persistance, mais l'estimation de ce point de référence requiert des quantités importantes de données et elle est sensible aux erreurs du taux de mortalité naturelle. Nous présentons une méthode d'estimation qui quantifie le changement de LEP produit dans une pêche lorsque seulement des échantillons de fréquences de longueurs, l'un tôt dans la pêche et l'autre récent, sont disponibles pour analyse. Basées sur des données de fréquences de longueur simulées avec des valeurs de paramètres connues, les estimations de LEP ont des erreurs non détectables lorsqu'on les confronte avec la variabilité de l'échantillonnage aléatoire et des tailles d'échantillons aussi petites que 100. Les simulations des données artificielles produisent, comme on peut s'y attendre, des estimations erronées lorsqu'on utilise (*i*) des paramètres de croissance différents de ceux du modèle d'estimation, (*ii*) des structures de tailles changeantes ou (*iii*) un recrutement variable. Par comparaison directe avec le point de référence du rapport du potentiel de fraye, LEP fractionnaire est beaucoup moins sensible aux erreurs de taux de mortalité naturelle. L'application de la méthode aux données de fréquences de longueurs du sébaste bleu (*Sebastes mystinus*) pour les années de 1980 à 2003, indique que dans cet intervalle de temps, les valeurs de LEP ont chuté de façon préoccupante.

[Traduit par la Rédaction]

Introduction

Persistence of populations requires that sufficient reproductive capacity be protected to achieve replacement. Yet, the result of virtually all fisheries is a decrease in spawning stock biomass and egg production through truncation of the age and size structure. The ability of a population to persist is most seriously jeopardized if the selectivity of the fishery removes individuals prior to spawning and allows little accumulation of individuals of reproductive size and age (Sissenwine and Shepherd 1987; Myers and Mertz 1998; Longhurst 2002). In cases where fisheries progressively select younger, smaller individuals over time, dramatic decreases in egg production can result, and the population's ability to persist is brought into question (Myers and Quinn 2002).

A variety of biological reference points are used by fisheries managers to set harvest targets, ensure persistence, and manage in a precautionary manner (Food and Agriculture Organization of the United Nations 1995). Following the precautionary approach, target reference points are set as goals for a fishery. Limit reference points (LRP) are threshold indicators of stock health that are not to be exceeded. While many possible LRPs have been identified (Caddy and Mahon 1995), to provide the best guarantee of sustainability, LRPs should directly reflect population persistence. Results from density-dependent, age-structured models demonstrate that maintenance of sufficient lifetime egg production (LEP) is necessary to ensure a nonzero equilibrium stock size (Sissenwine and Shepherd 1987).

The spawning potential ratio (SPR) (Gabriel et al. 1989; Goodyear 1993) is a commonly used biological reference point that describes the change in spawning stock biomass per recruit (SSBR) resulting from a fishery. SPR is the ratio

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M.R. O'Farrell[1] and L.W. Botsford. Department of Wildlife, Fish and Conservation Biology, One Shields Avenue, University of California, Davis, CA 95616, USA.

[1]Corresponding author (e-mail: mrofarrell@ucdavis.edu).

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of SSBR of a fished population to that of the population in the virgin, unfished state. In general, SSBR is assumed to be proportional to egg production per recruit. If this assumption is correct, SPR would describe how much egg production per recruit has changed owing to fishing and directly reflect population persistence.

Several attempts have been made to identify general levels of SPR to be used as reference points. Using groundfish life history parameters, Clark (1991) suggested that reducing spawning biomass per recruit to 35% of the unfished level could be a useful, safe management target. If variable recruitment was included with this analysis, using the same life history parameters, the recommended target SPR value was raised to 40% (Clark 1993). Mace and Sissenwine (1993) surveyed 91 stock–recruitment data sets and suggested that an SPR value of 30% could be used as a management "threshold" (i.e., an LRP). Mace (1994) later suggested that 40% is a plausible target value of SPR. The general similarity of these results led to many fisheries being managed at a level of fishing mortality rate (F) that reduced the SSBR to 35%–40% of the unfished SSBR ($F_{35\%}$, $F_{40\%}$). Groundfish on the Pacific coast of the United States were managed using $F_{35\%}$ as a target reference point until it became evident that many stocks of rockfishes (*Sebastes* spp.) were becoming badly depleted and stocks were not asymptotically approaching equilibrium (Ralston 2002). For less resilient stocks such as the rockfishes, a harvest strategy that ensures conservation of a larger proportion of SSBR is required (Brodziak 2002; Clark 2002; MacCall 2002). Dorn (2002) estimated a risk-averse target level of SPR for rockfishes between 55% and 60%.

The ability to calculate SPR is limited by data availability. Generally, SPR is calculated by estimation of F, natural mortality rate (M), and computation of SSBR from age-structured data. In rapidly developing fisheries, recreational fisheries, and fisheries deemed "unimportant", traditional catch, effort, and catch at age data may not be collected. Ageing fish can be expensive and time consuming. Little information about M may be available externally and data limitation may not allow for direct estimation. This can be particularly problematic, as SPR is highly sensitive to errors in M (Goodyear 1993). Size distributions are much less expensive to collect than age-structured data, and for many fisheries, the only data available are a few length distributions from the catch.

We describe a size-structured assessment method that estimates the fractional change in LEP (FLEP) between two size frequency distributions: one early in the exploitation history and the other current. The information required for the estimation procedure are two size distributions from the catch, an age–length relationship (e.g., von Bertalanffy), a length – egg production (or biomass) relationship, and an estimate of M. The estimated FLEP would be equivalent to SPR if the early size distribution were taken prior to the commencement of a fishery and spawning stock biomass were proportional to egg production.

In the remainder of this paper, we (*i*) describe the size-structured model and the estimation procedure, (*ii*) evaluate the performance of the estimation procedure with simulated data with various departures from assumptions, (*iii*) provide an example in which we compare FLEP and SPR estimates using data from blue rockfish (*Sebastes mystinus*) in northern California, and (*iv*) discuss the performance of this method and compare it with other methods for calculating reference points when data are limited.

Size-structured model

Growth

Estimation of LEP derives information from the size structure of a population, which is determined by growth, recruitment, and mortality. Here, we used the von Bertalanffy growth function to describe length at age, but other growth functions may be used if more appropriate for a particular stock (see Quinn and Deriso (1999) for descriptions of alternative growth functions). We incorporated growth rate variability explicitly by making the asymptotic length parameter (L_∞) a normally distributed random variable (Sainsbury 1980; Botsford et al. 1994; Smith et al. 1998). Prior work (Botsford et al. 1994) has shown that variation in the von Bertalanffy k parameter has little effect on equilibrium size structure, and thus, it was fixed for this model. The result of this form of growth variability was a normal distribution of lengths for each cohort. The degree of variation in length at age was adjusted by varying the coefficient of variation (CV) of L_∞. In all examples presented, we assumed CV L_∞ = 0.10 and the distribution of L_∞ was truncated at ±3 SDs, which is a plausible level of CV L_∞ for many rockfishes (e.g., Lea et al. 1999). Summing the size distribution of each cohort from age 0 to the maximum age observed produced a population size structure constructed with known growth parameters and a predetermined degree of variation in length at age (CV L_∞).

Recruitment and mortality

The size structure of a population is further shaped by the pattern of recruitment into the population and size-dependent mortality. Here, we assumed a constant level of yearly recruitment to the earliest age-class (age 0). Changes in abundance of each cohort therefore were strictly a function of mortality rates.

Mortality was divided into two types: natural mortality M and fishing mortality F. The M was specified as size independent and the only source of mortality prior to entry into the fishery:

$$(1) \qquad Z(l) = M \quad \text{for } l < l_c$$

where $Z(l)$ is total instantaneous mortality at length (l) and l_c is length at first capture in the fishery. This formulation selectively removes individual fish based on their size. The F at length is conditional on the type of gear used in the fishery. We assumed fishery selectivity to be asymptotic; F increased with size until a length at which fish were fully recruited to the gear. Where individuals were partially recruited to the fishery, F was discounted by a selectivity multiplier:

$$(2) \qquad Z(l) = M + S(l)F \quad \text{for } l_c \le l < l_r$$

where $S(l)$ is the selectivity ogive and l_r is length at full recruitment. We assumed a two-parameter, cumulative Gaussian selectivity ogive for all examples presented in this paper. Finally, when fully recruited into the fishery:

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$$(3) \qquad Z(l) = M + F \quad \text{for } l \geq l_c$$

Allowing the model to reach equilibrium and summing the size distribution of all cohorts produced a population size structure with known growth parameters and estimated harvest characteristics.

The estimated population size structure and length – egg production relationship were then used to calculate LEP:

$$(4) \qquad \text{LEP} = \sum_{l_{50}}^{l_{max}} N_l m_l$$

where N_l and m_l are abundance and fecundity at length, respectively. We assumed that all individuals equal to or larger than the length at 50% maturity (l_{50}) are fecund and that fecundity was an allometric function of length (i.e., $m_l = al^b$, where a and b are fixed parameters that vary by species). In the case where a length – egg production relationship is not available, a length–weight relationship may be substituted, as weight can be correlated with fecundity (Quinn and Deriso 1999).

LEP was calculated for two size distributions, one from early in the fishery (before major depletion) and one recent (after fishery development). FLEP was determined from the LEP values computed from the early size distribution and the recent size distribution with an assumption of constant recruitment:

$$(5) \qquad \text{FLEP} = \frac{\text{LEP}_{\text{recent}}}{\text{LEP}_{\text{earliest}}} = \frac{\text{LEP}_{\text{present}}}{\text{LEP}_{\text{unfished}}}$$

FLEP is a measure of the fractional change in egg production per recruit between the two size structures. It is analogous to the fraction of unfished LEP and SPR, with the exception that it does not provide an estimate of LEP prior to exploitation. Instead, it measures the change in LEP in the time interval for which data are available. In the application of this method, the early size structure should be obtained as close as possible to the beginning of the fishery and would most closely approximate the unfished state.

Estimation

The first step in the estimation procedure is to choose size boundaries for the selectivity of F. Without independent knowledge of the selectivity ogive, the size ranges over which F operates were somewhat arbitrarily chosen. We choose l_c and l_r a priori rather than including them in the estimation procedure for two reasons. First, the estimation procedure performed well using assumed values of l_c and l_r, even when incorrect values were assumed. Second, the estimation procedure performed inconsistently when including the two extra parameters, implying that the data did not contain enough information to reliably yield good estimates for the added parameters. Therefore, size boundaries for F were set by characteristics of the catch data in the following manner:

$$(6) \qquad F(l) = \begin{cases} 0, & l < l_c \\ S(l)F, & l_c \leq l < [l_{mode} + (l_{max} - l_{mode})/2] \\ F, & l \geq [l_{mode} + (l_{max} - l_{mode})/2] \end{cases}$$

where l_{mode} was the modal size in the catch size distribution (data) and l_{max} was the largest size observed in the catch size distribution. We set these size boundaries for the selectivity length range because l_{mode} is the result of (*i*) the size structure of the population and (*ii*) the shape of the selectivity ogive. It is possible for l_{mode} to occur at a length smaller than the length of full recruitment to the fishery for size structures where N_l declines sharply with increasing length. The length range of selectivity specified in eq. 6 allowed for this possibility, while the assumption of a narrower length range for the selectivity ogive would not.

With the size range of the F assumed, maximum likelihood estimates of three parameters were obtained from the catch data; F, μ_{sel} (the mean of the cumulative Gaussian selectivity ogive), and σ_{sel} (the standard deviation of the selectivity ogive) were estimated by finding the equilibrium population size structure with the combination of parameters that, when sampled by harvest, best fit the data (Fig. 1). The equilibrium population structure was sampled by harvest using the parameters of the population size structure:

$$(7) \qquad C(l) = \begin{cases} N(l)[1 - \exp(0)], & l < l_c \\ N(l)[1 - \exp(-S(l)F)], & l_c \leq l < [l_{mode} + (l_{max} - l_{mode})/2] \\ N(l)[1 - \exp(-F)], & l \geq [l_{mode} + (l_{max} - l_{mode})/2] \end{cases}$$

so that the best fit to the data was obtained (Fig. 1). Here, $C(l)$ is catch at length l and $S(l)$ is determined by the values of μ_{sel} and σ_{sel}. The catch size structure was therefore a representation of catch within each length bin.

Maximum likelihood estimates of F, μ_{sel}, and σ_{sel} were obtained by minimizing the separation statistic of Schnute and Fournier (1980) without their multiple of 2:

$$(8) \qquad \theta(F, \mu_{sel}, \sigma_{sel}) = \sum_{l=l_c}^{l=l_{max}} O_l \ln\left(\frac{O_l}{P_l}\right) \quad \text{for } O_l, P_l \geq 1$$

where O_l and P_l are the observed and predicted number of individuals at length l, respectively. The objective function was minimized using the Nelder–Mead simplex algorithm (Press et al. 1986), implemented with the MATLAB (Math Works 2002) library function "fminsearch". Initial starting parameters for the minimization were drawn from uniform distributions encompassing the true value of each parameter.

Evaluation of performance

Approach

We evaluated the performance of the estimation method using simulated data generated by the size-structured governing model described above. For all simulations, we used the von Bertalanffy parameter set, M estimate, maximum age, CV L_∞, and length–weight allometric relationship parameters (a and b) for female blue rockfish (Table 1).

Bias and variability in estimates of LEP were first examined for the baseline case where deterministic catch size distributions were randomly sampled with $n = 1000$, $n = 200$, and $n = 100$. Three levels of F (0.05, 0.20, and 0.50) were used in the simulation of artificial data to represent the range

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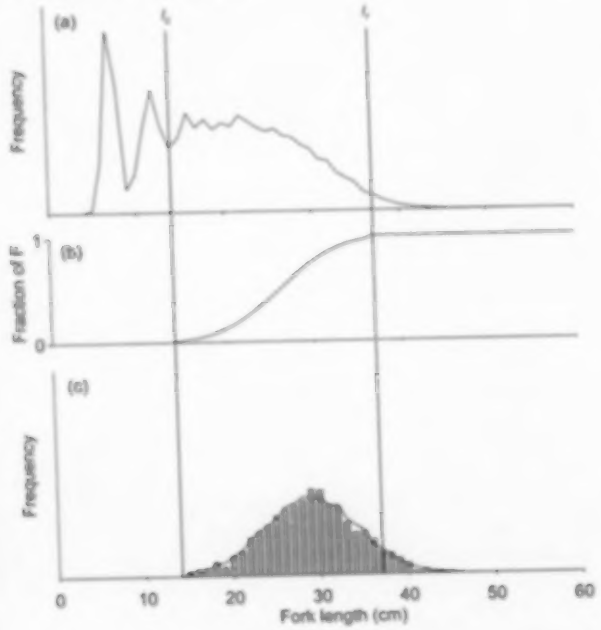
Table 1. Parameter set used to generate length frequency data.

Parameter	Value	Source	Definition
L_∞	40.02	Laidig et al. 2003	Asymptotic von Bertalanffy length
k	0.15	Laidig et al. 2003	von Bertalanffy growth parameter
t_0	−1.34	Laidig et al. 2003	Age at which individual would have been length 0
CV L_∞	0.10*	na	Coefficient of variation of L_∞
Maximum age	41	Laidig et al. 2003	Maximum age
M	0.10	Hoenig 1983	Natural mortality rate
a	0.0158†	Love et al. 2002	Coefficient of the allometric length–fecundity relationship
b	2.988†	Love et al. 2002	Exponent of the allometric length–fecundity relationship
l_{50}	28	Love et al. 2002	Length at 50% maturity
R	1000	na	Recruitment level
F	0.05, 0.20, 0.50	na	Fishing mortality rate
μ_{sel}	25	na	Mean of the selectivity ogive
σ_{sel}	5	na	Standard deviation of the selectivity ogive

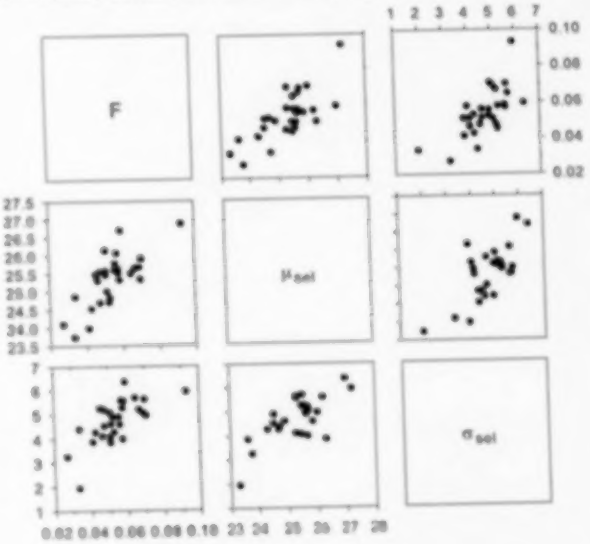
Note: na, not applicable.
*CV L_∞ is assigned a plausible value of 0.10, although this is not estimated from data.
†Allometric model parameters a and b correspond to the length–weight relationship for blue rockfish (*Sebastes mystinus*) but are assumed to represent the length–fecundity relationship for this species.

Fig. 1. Graphical description of the estimation procedure. (*a*) Population size structure. (*b*) Selectivity ogive. (*c*) Catch data (vertical bars) and estimated catch size structure (solid line). Vertical lines denote the length range over which the selectivity ogive operates, where l_c is the length at first capture and l_r is the length of full recruitment. Maximum likelihood estimates of parameters F (fishing mortality rate), μ_{sel} (the mean of the cumulative Gaussian selectivity ogive), and σ_{sel} (the standard deviation of the selectivity ogive) are produced by finding the equilibrium population size structure that, when sampled by harvest, produces the best fit to the data.



of exploitation expected in a fishery, from near-virgin (F = 0.05) to well-developed (F = 0.20) and heavily fished (F = 0.50). For each combination of sample size and F, 30 Monte Carlo data sets were generated. The distribution of the 30 estimates of LEP was then compared with the true value of LEP generated by the governing model.

Fig. 2. Regressions showing correlation between parameters estimated from simulated data. Parameter values are the result of estimates performed on 30 Monte Carlo data sets with F = 0.05, μ_{sel} = 25, σ_{sel} = 5, and n = 1000. F, fishing mortality rate; μ_{sel}, the mean of the cumulative Gaussian selectivity ogive; σ_{sel}, the standard deviation of the selectivity ogive.



We then generated data with a variety of departures from assumptions that could arise in a practical context. In the first case, data were generated with CV L_∞ smaller (0.05) and larger (0.15) than the CV L_∞ assumed in the estimation model (0.10). This scenario evaluated how precise the assumed variability in L_∞ must be to obtain accurate estimates of LEP.

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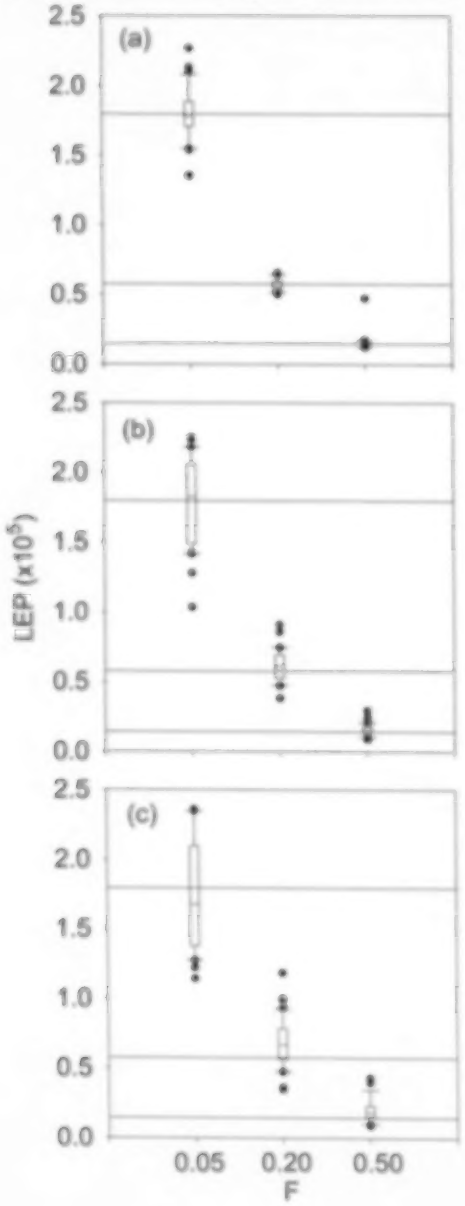
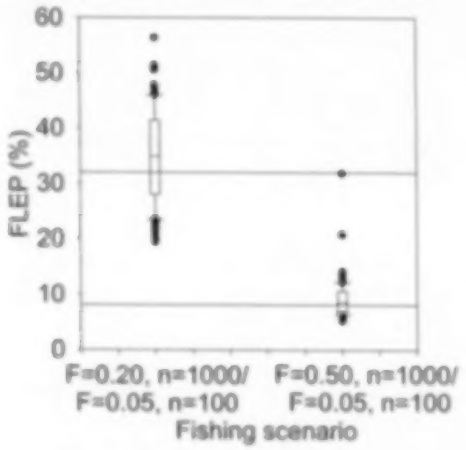
Fig. 3. Distributions of lifetime egg production (LEP) estimates from simulated data with three levels of fishing mortality rate (F) and sample size (*a*) n = 1000, (*b*) n = 200, and (*c*) n = 100. Each box is the result of 30 estimates from Monte Carlo data sets. Box plots display the median (center line), 25th to 75th percentiles (boxes), 10th and 90th percentiles (whiskers), and outliers (●). The horizontal lines represent true LEP values.



The second test considered the case where L_∞ in the governing model was set to 10% above and 10% below the value of L_∞ assumed in the estimation model. This evaluated whether a high level of accuracy in estimates of L_∞ was needed to produce accurate estimates of LEP. For both cases, 30 Monte Carlo data sets were generated for each value of F listed in Table 1. Distributions of LEP estimates were compared with the true value of LEP.

Fig. 4. Distribution of fractional lifetime egg production (FLEP) calculated from LEP distributions for two fishery scenarios: (*i*) the ratio of recent LEP with moderate fishing mortality rate (F = 0.20) and abundant data (n = 1000) to early LEP with light fishing (F = 0.05) and sparse data (n = 100) and (*ii*) the ratio of recent LEP with heavy fishing (F = 0.50) and abundant data (n = 1000) to early LEP with light fishing (F = 0.05) and sparse data (n = 100). Distributions of FLEP are computed from 100 random samples from the LEP distributions in Fig. 3. Box plots display the median (center line), 25th to 75th percentiles (boxes), 10th and 90th percentiles (whiskers), and outliers (●).



Another potential source of error in the estimation of LEP is the use of an equilibrium-based method when the size structure contains transient effects. Our estimation model assumes an equilibrium size structure, but recent changes in fishing and (or) selectivity in an actual population can result in transient size structures as new equilibria are approached. We generated transient size structures resulting from a shift in F, analogous to the instantaneous development of a new fishery. The ability of the equilibrium-based estimation method to produce accurate LEP estimates for transient size structures was then evaluated over the duration of the transient.

Next, we examined how the estimation method, which assumes a constant level of annual recruitment, performed on data generated with recruitment variability. Recruitment variability produces natural fluctuation in egg production over time. However, if mortality rates do not change, actual LEP will remain constant. To evaluate how fluctuations in egg production produced by recruitment variability affected estimates of LEP and FLEP, we simulated size distributions with lognormal recruitment variability with CVs typical of Pacific coast rockfishes (Fogarty 1993; Ralston and Howard 1995). We then examined actual variability in egg production produced by fluctuations in recruitment and evaluated whether this variability led to biased estimates of LEP and FLEP over a 20-year interval.

Finally, we investigated the sensitivity of FLEP to a misspecification of M. Goodyear (1993) demonstrated that errors in externally estimated values of M could lead to significant biases in the estimate of SPR. To determine if the FLEP method was as sensitive to M as SPR, we generated

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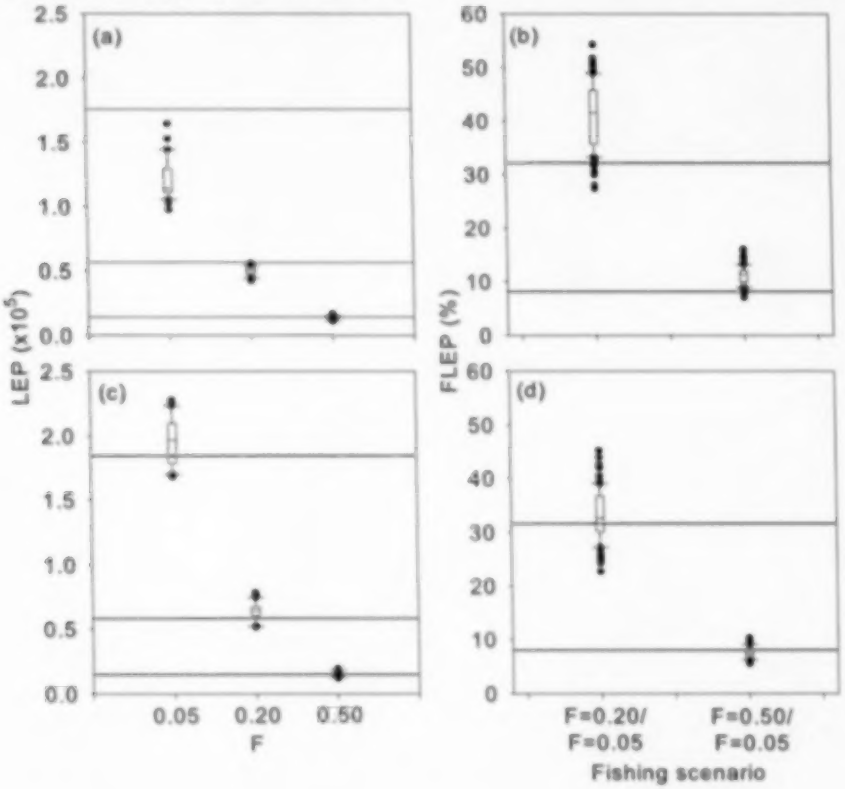
Fig. 5. Lifetime egg production (LEP) and fractional LEP (FLEP) distributions when the coefficient of variation of the asymptotic length parameter (CV L_∞) for generated data is (*a* and *b*) less than (0.05) and (*c* and *d*) greater than (0.15) the CV L_∞ of the estimation model (0.10). LEP distributions are the result of estimates from 30 Monte Carlo data sets with $n = 1000$. FLEP distributions are computed from 100 random samples from the LEP distributions. Horizontal lines represent true LEP and FLEP values. Box plots display the median (center line), 25th to 75th percentiles (boxes), 10th and 90th percentiles (whiskers), and outliers (●). Fishery scenarios presented in the distribution of FLEP are (*i*) the ratio of LEP with low fishing mortality (F) to moderate F ($F = 0.05$ to $F = 0.20$) and (*ii*) the ratio of LEP with low F to heavy F ($F = 0.05$ to $F = 0.50$).



size structures with a range of M values and performed the estimation procedure with an assumed value of M (0.10). SPR was calculated by dividing the estimated LEP values by a virgin LEP value obtained by setting $F = 0$. Sensitivity results for FLEP were compared with sensitivity results for SPR.

Results

The calculation of LEP is contingent on estimates of F, μ_{sel}, and σ_{sel}, which describe the harvest characteristics and the shape of population size distribution. We display how F, μ_{sel}, and σ_{sel} covaried for a representative set of 30 estimates ($F = 0.05$, $\mu_{sel} = 25$ cm, $\sigma_{sel} = 5$ cm, $n = 1000$) (Fig. 2). These correlations suggested that a good fit to the data could be produced by more than one parameter combination. For example, fishing at a high rate with a shallow selectivity ogive can produce a size structure similar in shape to one produced by fishing at a lower rate with a steeper selectivity ogive. However, the ultimate goal of the procedure is to produce accurate estimates of LEP, which may be accomplished even when the underlying parameter estimates are correlated. In the following sections, we examine the accuracy and precision of LEP estimates, which were a product of the maximum likelihood estimates of F, μ_{sel}, and σ_{sel}.

The method generally produced estimates of LEP with undetectable bias for the baseline case where sampling variation and low sample sizes were the only challenges to the procedure (Fig. 3). Substantial biases were not detected, as the true value of LEP fell within the interquartile range of the distributions for each case considered. Estimates were more precise at higher levels of F and larger sample sizes.

To investigate the degree to which the variation in estimates of LEP would affect variability in FLEP, we compared populations that were ultimately heavily fished with lightly fished populations. In both, we assumed that early sample sizes were small and fishing light (approximating sparse data from early in a fishery's development) and recent sample sizes were large with heavier F (approximating a more developed fishery and sampling program). One hundred LEP values were randomly sampled from the distribution of LEP estimates for $F = 0.05$, $N = 100$ (early estimates) and the distributions of LEP estimates for $F = 0.50$, $N = 1000$ and $F = 0.20$, $N = 1000$ (recent estimates). The resulting distri-

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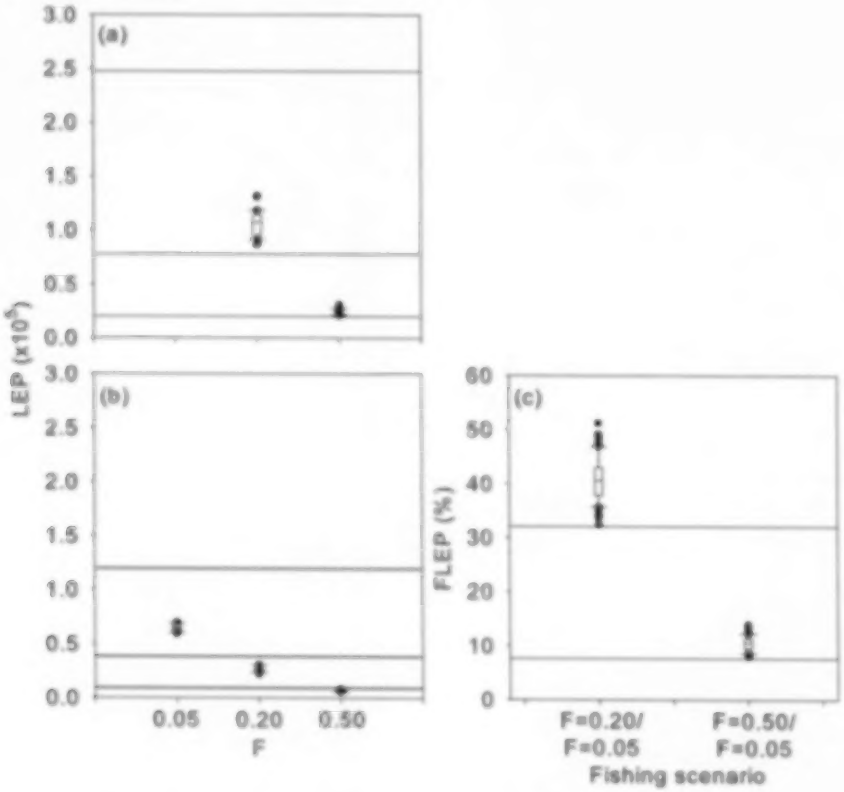
Fig. 6. Lifetime egg production (LEP) and fractional LEP (FLEP) distributions when the asymptotic length parameter (L_∞) of generated data is (*a*) 10% greater than and (*b* and *c*) 10% less than the L_∞ of the estimation model. LEP distributions are the result of estimates from 30 Monte Carlo data sets with $n = 1000$. FLEP distributions are computed from 100 random samples from the LEP distributions. No estimates of LEP could be made for fishing mortality rate (F) = 0.05 when L_∞ was 10% greater than the estimation model (Fig. 6*a*). As a result, no estimates of FLEP could be made for the two fishing scenarios at this value of L_∞. Box plots display the median (center line), 25th to 75th percentiles (boxes), 10th and 90th percentiles (whiskers), and outliers (●). Fishery scenarios presented in distribution of FLEP are (*i*) the ratio of LEP with low F to moderate F ($F = 0.05$ to $F = 0.20$) and (*ii*) the ratio of LEP with low F to heavy F ($F = 0.05$ to $F = 0.50$).



butions of FLEP were generally unbiased, as the true values were within the interquartile range of the distributions (Fig. 4). The degree of precision in the FLEP estimates was contingent upon the variability of the distribution of the component LEP estimates. A less variable distribution of FLEP estimates can be produced by decreasing variation in the LEP estimates through increased sample sizes. For example, if we had used the $F = 0.05$, $N = 1000$ distribution (Fig. 3*a*) of estimates as our "early" condition, distributions of FLEP would be less variable.

When there is a disparity between CV L_∞ assumed in the estimation model and the CV L_∞ that produced the data, estimates of LEP can be biased (Fig. 5). The distribution of LEP estimates for the case where data were generated with a CV L_∞ smaller than the CV L_∞ assumed in the estimation model was negatively biased for all levels of F. This bias can be attributed to the paucity of large individuals present in the simulated catch distribution, a result of the narrower distribution of size at age, being interpreted as a result of increased F by the estimation model. The increase in estimated F results in a decrease in the estimate of LEP. Negatively biased estimates of LEP resulted in positively biased estimates of FLEP (Fig. 5). Biases in LEP estimates were not detected when the CV L_∞ of generated data was larger than the value assumed in the estimation model. As a result, no bias in FLEP values was observed (Fig. 5).

Biased estimates of LEP were also observed if the value of L_∞ assumed was 10% higher or lower than the actual value (Fig. 6). When L_∞ of the data was higher than in the estimation model, estimates of LEP were biased high. In this case, a preponderance of larger individuals (as a result of the higher value of L_∞) is interpreted by the estimation model to be the result of low F (i.e., more fish are living to a large size). As a result of low estimates of F, estimates of LEP were biased high. An extreme case of this is apparent in Fig. 6*a*, where no estimate of LEP could be made for $F = 0.05$. Here, it is essentially impossible to make F low enough to observe the large individuals present in the data, and the estimation fails. Biases in LEP were opposite in direction where L_∞ was 10% lower in the data than in the estimation model. In both cases, larger biases in LEP were observed for lower levels of F. As a result, estimates of

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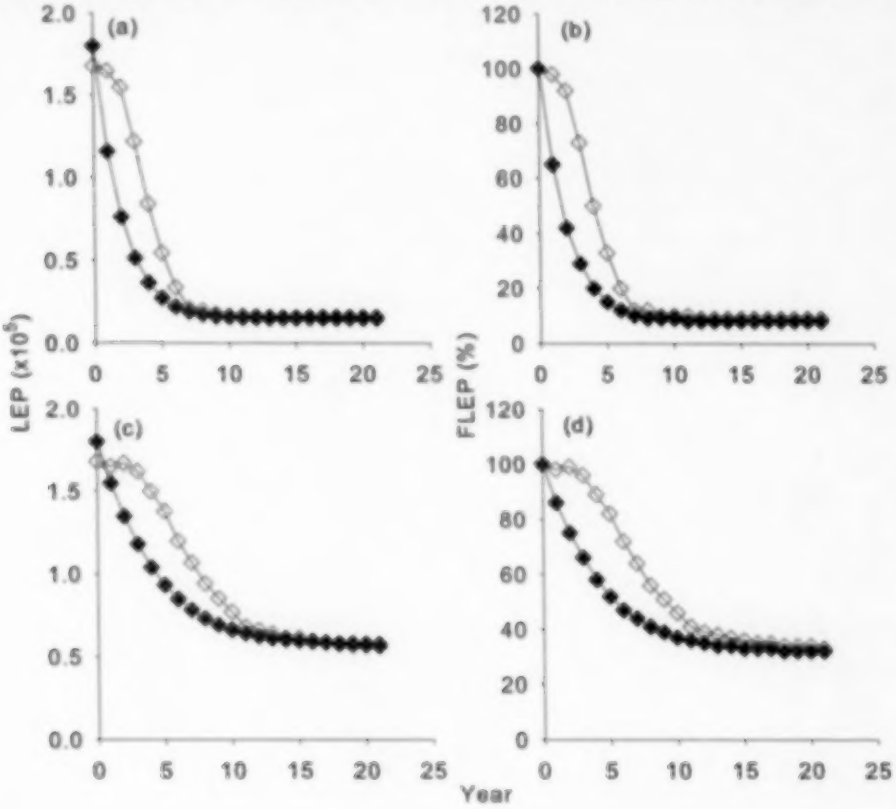
Fig. 7. Time series of true value (solid diamonds) and estimated values (open diamonds) of lifetime egg production (LEP) and fractional LEP (FLEP). (*a* and *b*) Transient changes resulting from an instantaneous shift from fishing mortality rate (F) = 0.05 to F = 0.50 in year 1. (*c* and *d*) Transient changes resulting from an instantaneous shift from F = 0.05 to F = 0.20 in year 1.



FLEP were biased high for the two fishing scenarios presented (Fig. 6).

Estimation of LEP from transient size structures with this equilibrium-based estimation model resulted in biases when F was abruptly increased (Fig. 7). The two cases displayed show (*i*) the duration of the transient and (*ii*) estimation biases as LEP decreases for each year between equilibrium values for two levels of shifts in F (Fig. 7). First, transient dynamics were shorter in duration when the change in F was greater. The high value of F rapidly depleted fishable-sized individuals and decreased the number of age-classes in the fishable size range. Second, the shift in F was apparent as a lag in the estimate of LEP relative to actual LEP. The high bias resulted from lightly fished cohorts growing through the size structure.

Variable recruitment resulted in variability in egg production. A strong year-class entering at year 0 produces an increase in egg production after a lag time allowing the cohort to grow to reproductive size. The result of lognormally distributed recruitment variability on actual egg production, and estimates of LEP, is displayed in Fig. 8. For each level of F and recruitment variability, gradual shifts in egg production resulted as cohorts of unequal abundance grew into the reproductive size range. The magnitude of changes in egg production owing to recruitment variability was dependent on F. At higher F, the absolute variability in egg production, and estimates of LEP, owing to recruitment variability was smaller. This reflects the truncation of size structure produced by heavy fishing; even very strong cohorts are not able to have a large effect on egg production because the range of reproductive sizes present under high levels of fishing is small.

Estimated LEP lagged behind the time series of actual egg production and fluctuated about the true value of LEP (Fig. 8). The lag of LEP estimates behind the time series of egg production can be understood by examining how the size-structured model estimates F. As a large recruitment pulse moves into the catch size structure (data), the resulting size distribution contains many small individuals relative to large individuals. While this is a result of variable recruitment, the estimation procedure perceives this as an increase in F, since estimated mortality is the result of a formal comparison between large and small individuals. As a result, F is biased high and LEP is biased low. The bias shifts direction as the recruitment pulse moves through the size structure (e.g., Morgan et al. 2000). When the strong recruitment pulse has moved into the largest size-classes, the preponderance of large individuals is interpreted as a decrease in F

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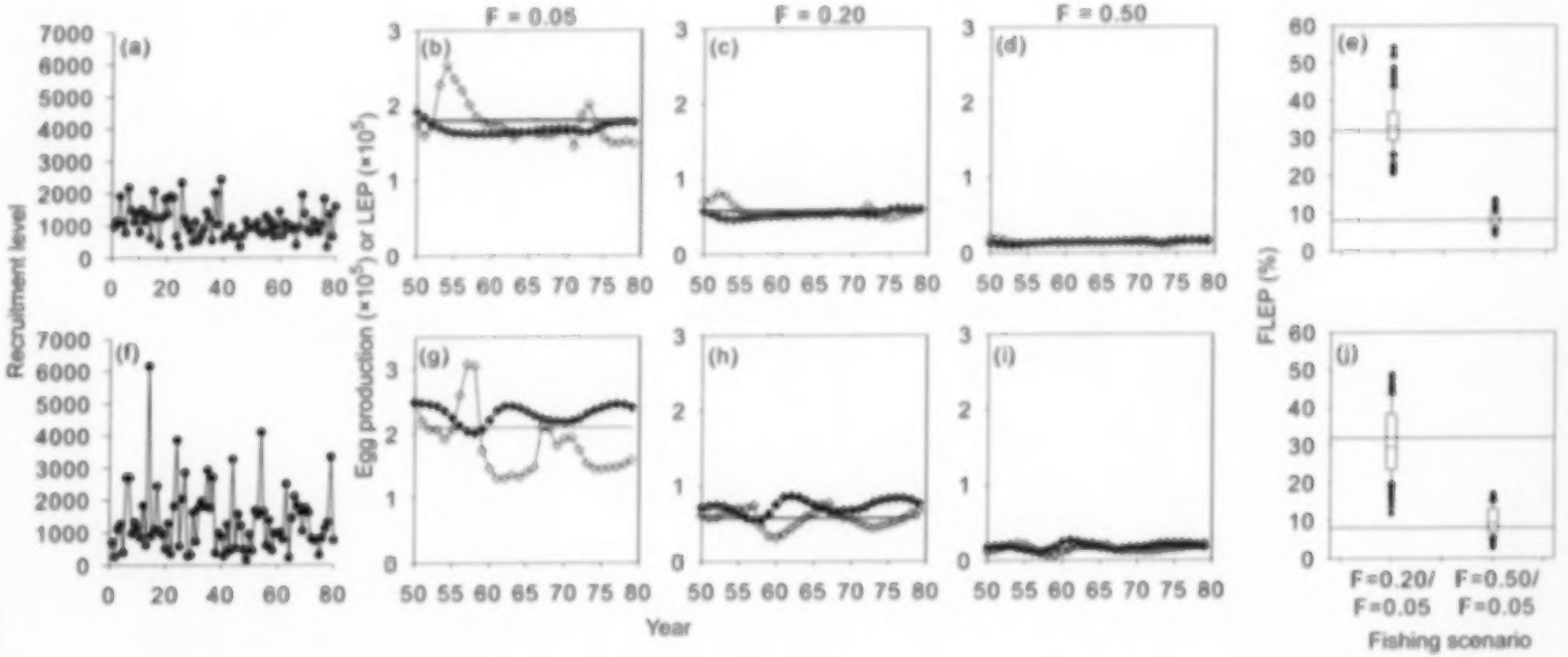
Fig. 8. Variability in recruitment, resulting variability in egg production, estimates of lifetime egg production (LEP), and fractional LEP (FLEP) distributions for two fishing scenarios are shown. Recruitment time series from year 0 to year 80 for recruitment (*a*) CV = 0.5 and (*f*) CV = 1.0. Actual values of egg production (solid diamonds), estimated values of LEP (open diamonds), and actual values of LEP (straight line) for years 50–80 for recruitment (*b*, *c*, and *d*) CV = 0.5 and (*g*, *h*, and *i*) CV = 1.0 at three levels of fishing mortality rate. (*e* and *j*) Resulting distributions of FLEP estimates for CV = 0.5 and CV = 1.0. FLEP distributions are computed from 100 random samples from the LEP distributions. Box plots display the median (center line), 25th to 75th percentiles (boxes), 10th and 90th percentiles (whiskers), and outliers (●). Fishery scenarios presented in distribution of FLEP are (*i*) the ratio of LEP with low fishing mortality (*F*) to moderate *F* (*F* = 0.05 to *F* = 0.20) and (*ii*) the ratio of LEP with low *F* to heavy *F* (*F* = 0.05 to *F* = 0.50).



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and, as a result, LEP is biased high. When examining time series of LEP estimates with simulated egg production, the resulting pattern is the time lag evident (Fig. 8).

Although recruitment variation resulted in estimates of LEP fluctuating about the true values of LEP, estimates of FLEP had undetectable bias (Fig. 8). Precision of FLEP estimates depended on the level of recruitment variation as more precise estimates of FLEP were obtained in the recruitment CV = 0.5 case.

Estimation of FLEP is much less sensitive to M than traditional SPR estimates (Fig. 9). Similar to Goodyear (1993), we find that SPR estimates are highly sensitive to an erroneous estimate of M. However, FLEP estimates over the same range of M vary little. The decreased sensitivity to M for the FLEP method can be attributed to the procedure of estimating virgin or baseline LEP from the data rather than calculating a virgin LEP by setting $F = 0$ (using an incorrect value of M). Estimating the baseline LEP value allows the F parameter to partially absorb the discrepancy in M between the data and the estimation model. As a result, the estimated total mortality rate (Z) is, in general, equal to the true Z.

Example: northern California blue rockfish

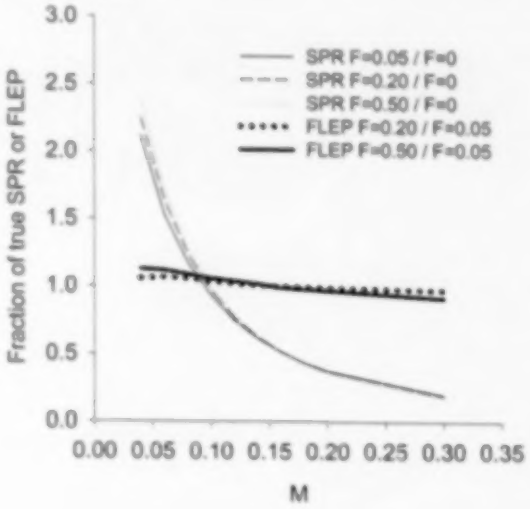
Blue rockfish is a common, nearshore rockfish that can dominate kelp forest fish communities in northern California (Love et al. 2002). The fishery for blue rockfish in California is predominantly recreational, with sport fishermen taking more than 90% of total landings from 1980 to 1989 and approximately 80% of the landings from 1993 to 2000 (Schroeder and Love 2002). There is some cause for concern for the health of blue rockfish stocks in California. In southern California, declines in recreational catch-per-unit-effort and shifts toward smaller individuals present in the catch since 1980 have been documented (Love et al. 1998). We applied the size-structured estimation method to length frequency data for blue rockfish in northern California from the sport catch. Data were obtained from the Marine Recreational Fisheries Statistics Survey and are publicly available from the Recreational Fisheries Information Network web site (http://www.psmfc.org/recfin/). Length frequencies were the product of sampler-examined catch from all fishing modes of the recreational fishery from Monterey County (central California) to the Oregon border.

Uncertainty in estimates of LEP (and thus FLEP and SPR) owing to random resampling of the data was represented by performing the estimation procedure on 30 bootstrapped size frequency distributions for each year (Press et al. 1986; Efron and Tibshirani 1991). For the FLEP example, the baselines were the LEP estimates from the 30 bootstrapped 1980 data set. For the SPR example, the baseline was the calculated LEP value when $F = 0$.

Model fits to the data varied in quality (Fig. 10). For 1981 and 2002, convergence to a single minimum of the separation statistic could not be obtained. In cases where distinct age-class effects (possibly caused by relatively large recruitment events) were evident, the model fit the data poorly (e.g., 2003). However, good fits were obtained for most years where size distributions lack obvious cohort size modes.

Both estimates of FLEP and SPR show a general decline since 1980 (Fig. 11). The most recent estimates of FLEP (from 1993 to 2003) fall within the range of concern if year 1980 is considered to be the virgin state. However, the SPR reference point estimates nearly all fall below 35%, suggesting that LEP was significantly reduced by fishing prior to 1980 and continuing through to 2003.

Fig. 9. Sensitivity of fractional lifetime egg production (FLEP) and spawning potential ratio (SPR) estimates to natural mortality rate (M). The estimation model assumed $M = 0.10$, while M varied in the artificial data from $M = 0.04$ to $M = 0.30$. SPR estimates were made by calculating the ratio of LEP at three levels of fishing mortality rate (F) to virgin LEP ($F = 0$). Two scenarios of FLEP are presented: (*i*) a shift from low to moderate F ($F = 0.05$ to $F = 0.20$) and (*ii*) a shift from low to high F ($F = 0.05$ to $F = 0.50$).



Discussion

We have described a size-structured method for estimation of change in LEP that does not require expensive, and often unavailable, catch at age data. The method allows a quantitative description of how changes in size structure affect persistence when sample size is not representative of total abundance. Finally, the calculation of FLEP is analogous to calculation of SPR, a reference point with strong theoretical support (Williams and Shertzer 2003).

Testing of the estimation procedure with various departures from assumptions identified the conditions under which estimation errors could arise. First, good estimates of von Bertalanffy parameters are desired, yet direction and magnitude of biases were identified if parameters are misspecified. Second, underestimation of CV L_∞ may lead to biased estimates of LEP. However, utilizing a higher value of CV L_∞ in the estimation model than is present in the population resulted in estimates of LEP with undetectable bias. This result suggests that using a higher value of CV L_∞ in the estimation model than is suspected for the population could reduce the probability of making biased LEP estimates. Third, transient shifts in LEP owing to a rapid change in F were not tracked perfectly by this equilibrium-based method. We demonstrated how LEP estimates tracked changes in the

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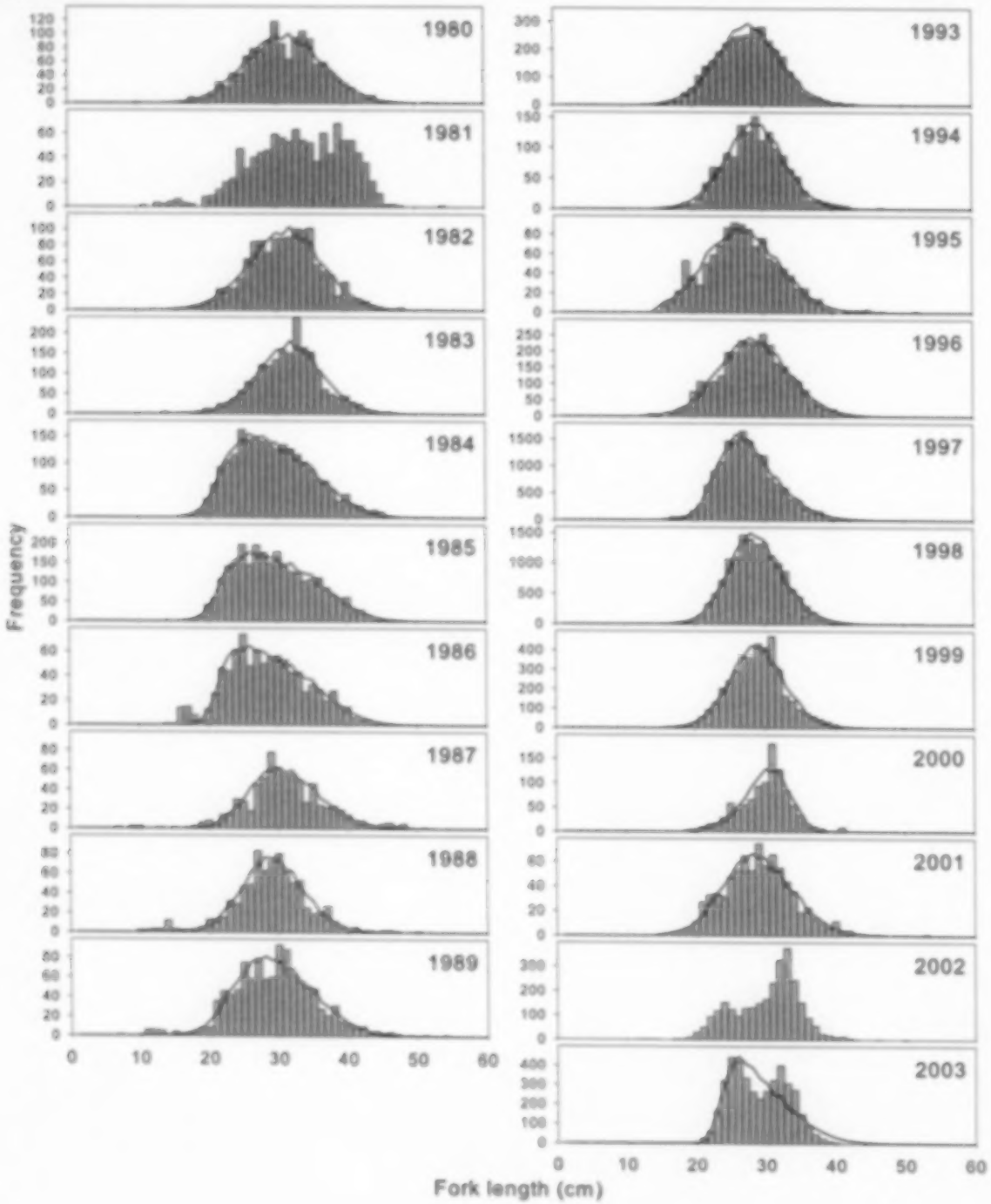
Fig. 10. Length frequencies from the recreational catch for blue rockfish (*Sebastes mystinus*) in northern California from 1980 to 2003 (no data are available from 1990 to 1992). Bars are size-structured data and lines are model fits. The estimation procedure failed to converge in 1981 and 2002.



true value of LEP with an instantaneous shift in F. A more realistic simulation of an actual fishery would instead show a rapid, but incremental, shift in F. The biased LEP estimates that resulted from this instantaneous shift in F therefore represent the most drastic biases that would be expected owing to transient dynamics. The effect of recruitment vari-

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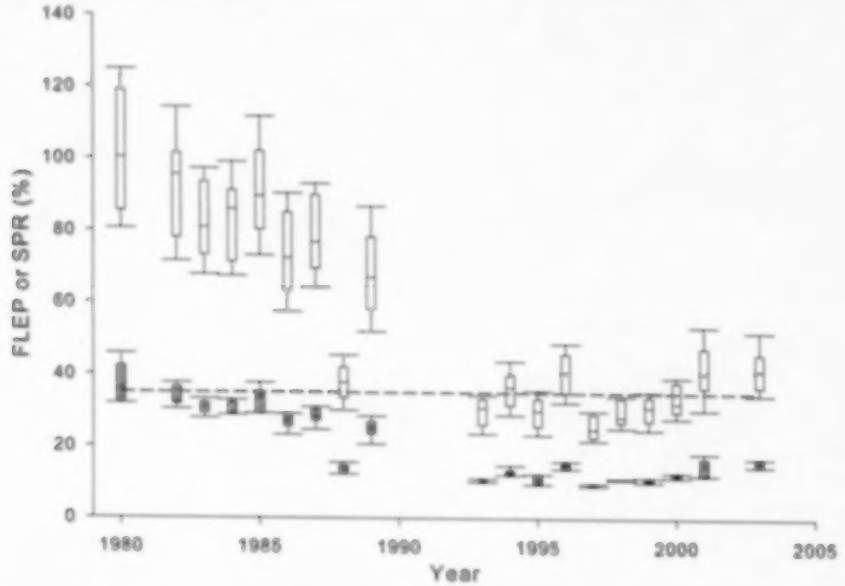
Fig. 11. Time series of fractional lifetime egg production (FLEP) (open boxes) and spawning potential ratio (SPR) (shaded boxes) estimated from 30 bootstrapped replicates of the data in Fig. 10. The broken line denotes FLEP = 35%. No data exist from 1990 to 1992. Convergence failures did not allow estimation in 1981 and 2002. Box plots display the median (center line), 25th to 75th percentiles (boxes), and 10th and 90th percentiles (whiskers).



ability on natural changes in egg production and estimates of LEP demonstrated that errors in estimation were small when F was high, and errors could be large when F was low. This issue may be most problematic when LEP estimates are attempted for early size structures (where F is very low) of populations that exhibit a large degree of recruitment variability. Cases where recruitment variability is very high may require other methods of mortality rate estimation such as following length frequency cohorts through time. However, for the two levels of recruitment variation explored here, estimates of FLEP lacked detectable bias. Finally, estimation of FLEP is much less sensitive to M than SPR. This result is particularly encouraging for management of data poor fisheries where good estimates of M are likely unavailable.

In the blue rockfish example, we represented random sampling error in the data using the bootstrap, resulting in a distribution of 30 LEP estimates for each year. The greater apparent precision of SPR estimates relative to FLEP estimates in Fig. 11 is the result of differences in how SPR and FLEP are calculated. For the SPR estimates, unfished LEP is a single value, calculated by setting $F = 0$ in the size-structured model. Therefore, the distribution of SPR estimates for each year of Fig. 11 is the result of 100 random choices of estimated LEP for each year (LEP_{recent}) divided by a single, calculated value for $LEP_{unfished}$. FLEP is the result of 100 random choices of LEP estimates for each year (LEP_{recent}) divided by 100 random choices from estimates of LEP in 1980 (the earliest available data, $LEP_{earliest}$). As a result of the inability to estimate $LEP_{unfished}$ from data with random sampling variability, the distribution of SPR estimates calculated here underrepresents the actual variability of this reference point.

In addition to differences in precision between FLEP and SPR in the blue rockfish example, there is a difference in the magnitude of the two reference points. We offer two hypotheses to explain why SPR estimates are consistently smaller than FLEP estimates in this example. First, the lower estimates of SPR relative to FLEP could reflect significant reduction of LEP prior to 1980. Very little quantitative data exist to evaluate this hypothesis formally, yet evidence points to an active recreational fishery before 1980. In northern and central California, blue rockfish was the numerically most dominant fish species in the party boat, skiff, and skin-diving catch during the years 1958–1961 (Miller and Gotshall 1965). However, length frequency distributions collected during this period (using different protocols than the data used here) do not differ substantially from the length frequency distribution from 1980 (Karpov et al. 1995). Ultimately, we simply do not know how much LEP had been reduced prior to 1980. A second hypothesis for the discrepancy between SPR and FLEP estimates is the extreme sensitivity of SPR to M. In the blue rockfish example, SPR estimates are approximately 40% of the FLEP estimates. If we momentarily assume that the FLEP estimates represent the true decline in LEP from the unfished state, an error of this magnitude could be the result of a relatively small error in the assumed M. An SPR estimate that is 40% of the true value would be the result of assuming $M = 0.10$ in the estimation, with the true M of the population being approximately 0.19. Given the difficulty in estimating M for nearly all populations, errors of this sort are certainly possible. We suggest viewing the FLEP estimates as an absolute minimum decline in LEP from the unfished state that are robust to misspecification of M.

Convergence failures in the minimization procedure demonstrate that more than one solution can exist for the same data set. Here, we did not reject alternative solutions based on biological grounds, as suggested by Schnute and Fournier

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(1980). Rather, if a single minimum value of the separation statistic was not located, we declared that a convergence failure occurred (e.g., 1981 and 2002). Workable parameter estimates can, however, be obtained by adding penalties to the objective function when parameters enter into a biologically implausible space (Hilborn and Mangel 1997).

Estimates of both FLEP and SPR depend on accurate specification of fecundity. For SPR to directly reflect persistence, egg production must be proportional to spawning stock biomass. In the blue rockfish example, we made the assumption that egg production was proportional to spawning stock biomass, yet this may be incorrect. For example, Love et al. (1990) demonstrated that the *b* parameter in the allometric relationship between length and fecundity is often larger than *b* in the length–weight relationship for several species of rockfishes, implying that fecundity increases with length faster than biomass increases with length. If this scenario exists, yet is not accounted for, any measure of change in egg production per recruit (by calculation of either SPR or FLEP) would be underestimated and the stock would appear to be healthier than it may actually be. Collection of reproductive individuals and establishment of length–fecundity relationships are a solution to this problem.

Recent results suggest that maternal age can be a better predictor of larval production than maternal size in black rockfish (*Sebastes melanops*) (Berkeley et al. 2004). Here, reduction in the number of older females owing to fishing would result a greater loss of reproductive capacity than would be expected by the equivalent loss in spawning stock biomass. If FLEP was used as a proxy to measure change in lifetime larval production, and maternal age effects were present, FLEP would be overestimated. Again, this would suggest that the stock is healthier than it truly is. However, if a maternal age effect is known to exist for a particular species, it can be readily included in the estimation procedure, since our model is both age and size structured. FLEP with the included maternal age effect would better represent changes in lifetime larval production, since the maternal age effect is a deviation from the assumption that egg production is proportional to spawning stock biomass.

Despite the potential sources of error identified and discussed above, this method is an improvement over other methods of calculating reference points when data are sparse. Surplus production models are often used to calculate reference points when limited data (catch, effort, catchability) are available. Gabriel and Mace (1999) advocated using the maximum sustained yield as an LRP when data are limited. Mace (2001) provided five reasons to use maximum sustained yield as an LRP. However, LRPs based on surplus production models do not directly reflect persistence. While fishing down the accumulated, old-growth biomass immediately decreases LEP, surplus production models are not able to detect this change in the stock's persistence (Botsford et al. 2004). However, the FLEP method is able to recognize the shift in size structure and resulting change in LEP.

This method may best be suited for evaluating persistence for long-lived, iteroparous populations where accumulated age and size structure is necessary for maintenance of sufficient levels of LEP. Unstructured models will be unlikely to detect a change in persistence as accumulated biomass and potential egg production are harvested from such populations. Collection of a small amount of data (length frequency, basic growth, and fecundity information) at the beginning of a fishery could allow FLEP estimates to closely approximate the SPR reference point.

Many biological reference points, including SPR, are sensitive to the productivity of the stock, defined by the steepness of the stock–recruitment relationship (Clark 2002; Myers et al. 2002; Williams and Shertzer 2003). Newly developed and data-poor fisheries will not have stock–recruitment data with sufficient contrast to allow for inference of stock productivity. FLEP can be used as an LRP while age-structured and stock–recruitment data are collected. Following the precautionary approach (Food and Agriculture Organization of the United Nations 1995), lower limits of FLEP for a fishery may be set a priori, and stock status can be estimated each year while more information is gathered. FLEP may be used as an LRP until stock–recruitment and catch at age data are sufficiently abundant to make more detailed stock assessments.

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Eggs-per-recruit model for management of the California market squid (*Loligo opalescens*) fishery

Michael R. Maxwell, Larry D. Jacobson, and Ramon J. Conser

Abstract: We develop a per-recruit model for the management of the California market squid (*Loligo opalescens*) fishery. Based on recent confirmation of determinate fecundity in this species, we describe how catch fecundity (i.e., eggs remaining in the reproductive tracts of harvested females) can be used to simultaneously infer fishing mortality rate along with management reference points such as yield-per-recruit, spawned eggs-per-recruit, and proportional egg escapement. Rates of mortality and egg laying have important effects on these reference points. Somewhat surprisingly, increasing the rate of natural mortality decreased spawned eggs-per-recruit while increasing proportional egg escapement. Increasing the rate of egg laying increased both spawned eggs-per-recruit and egg escapement. Other parameters, such as the maturation rate and gear vulnerability of immature females, affected the reference points. In actual practice, the influence of these parameters for immature squid may go undetected if immature squid are excluded from analysis of the catch. Application of this model to routine management is feasible but requires refinement of sampling procedures, biological assumptions, and model parameters. This model is useful because it is grounded on empirical data collected relatively inexpensively from catch samples (catch fecundity) while allowing for the simultaneous calculation of instantaneous fishing mortality rate and egg escapement.

Résumé : Nous mettons au point un modèle basé sur les recrues individuelles pour l'aménagement de la pêche commerciale du calmar opale (*Loligo opalescens*) de Californie. Nous basant sur la confirmation récente du déterminisme de la fécondité chez cette espèce, nous décrivons comment la fécondité de capture (c'est-à-dire le nombre d'oeufs qui restent dans le système reproducteur des femelles capturées) peut servir à la fois à déduire le taux de mortalité due à la pêche et certains points de référence de gestion, tels que le rendement par recrue, les oeufs pondus par recrue et l'échappement proportionnel des oeufs. Les taux de mortalité et de ponte ont des effets importants sur ces points de référence. De façon un peu inattendue, un accroissement du taux de mortalité naturelle diminue le nombre d'oeufs pondus par recrue, tout en augmentant l'échappement proportionnel des oeufs. Un accroissement du taux de ponte augmente à la fois les oeufs pondus par recrue et l'échappement des oeufs. D'autres variables, telles que le taux de maturation et la vulnérabilité des femelles immatures aux engins de pêche, affectent les points de référence. Dans la pratique, l'influence de ces variables peut passer inaperçue si les jeunes calmars sont exclus de l'analyse de la récolte. Il est possible d'utiliser notre modèle dans la gestion courante, mais il faut raffiner les techniques d'échantillonnage, les présuppositions biologiques et les paramètres du modèle. Le modèles est utile, car il est basé sur des données empiriques qui peuvent être assemblées à faible coût à partir d'échantillons de la capture (fécondité de capture), tout en permettant le calcul simultané de la mortalité instantanée due à la pêche et l'échappement des oeufs.

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Introduction

Fishing pressure on marine populations greatly increased in the 1990s (National Research Council 1994; Pauly et al. 1998). During this time, cephalopod fisheries emerged from dormancy to economic importance in many countries, compensating for declining catches in finfish fisheries (Lipinski et al. 1998). In recent years, squids have comprised the bulk of global cephalopod catch (Lipinski et al. 1998).

Despite the increasing importance of squid stocks, their assessment and management remain difficult problems (Beddington et al. 1990; Pierce and Guerra 1994; Lipinski et al. 1998). Many squids are capable of rapid and plastic growth, often completing their life cycles in less than 1 year (Boyle

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M.R. Maxwell.[1,2] University of California, San Diego, c/o Southwest Fisheries Science Center, 8604 La Jolla Shores Drive, La Jolla, CA 92037, USA.
L.D. Jacobson. National Marine Fisheries Service, Northeast Fisheries Science Center, 166 Water Street, Woods Hole, MA 02543-1097, USA.
R.J. Conser. National Marine Fisheries Service, Southwest Fisheries Science Center, 8604 La Jolla Shores Drive, La Jolla, CA 92037, USA.

[1]Corresponding author (e-mail: maxwellm@sandiego.edu).
[2]Present address: Department of Biology, University of San Diego, 5998 Alcalá Park, San Diego, CA 92110, USA.

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1990; Lipinski 1998). Subannual life cycles mean that population abundance at any given time depends on previous short-term spawning success and subsequent survival of offspring (Beddington et al. 1990). Environmental conditions may impact recruitment strength in squid (Robin and Denis 1999; Agnew et al. 2000; Waluda et al. 2002), contributing to substantial interannual variation in population abundance (Caddy 1983; Pauly 1985; Boyle and Boletzky 1996). The lack of biomass carryover from one year to the next casts doubt on the applicability of management approaches and models developed for longer-lived fish to short-lived squid stocks.

Because squid population abundance often hinges on previous spawning success and subsequent recruitment, several squid fisheries are managed by within-year or within-season approaches. These approaches typically do not attempt to predict future squid abundance. Rather, the focus is the current population or hypothesized cohort, with management allowing for sufficient "reproductive escapement" to produce subsequent generations (Beddington et al. 1990; Rosenberg et al. 1990; Brodziak and Rosenberg 1993). The appropriate level of escapement in absolute numbers of eggs or larvae may be unknown, so escapement is expressed as "proportional escapement": the reproductive output of the fished population relative to the expected output in the absence of fishing (Beddington et al. 1990). When estimates of egg or larval production are lacking, spawning biomass and (or) population abundance are used as indices of reproductive output. Currently, some squid fisheries employ modified depletion models to achieve management goals of maintaining stock abundance above an absolute or relative escapement threshold. Examples include fisheries for *Illex argentinus* (Rosenberg et al. 1990; Basson et al. 1996; Barton et al. 2004) and *Loligo gahi* (Agnew et al. 1998; Hatfield and Des Clers 1998) off the Falkland Islands (also see Brodziak and Rosenberg 1993).

Management based on depletion models is relatively data intensive, requiring series of within-season estimates of population abundance to calculate escapement (Beddington et al. 1990). Because such analyses depend on reliable temporal data, they often do not provide an estimate of escapement until the end of the fishing season (Agnew et al. 2000). Alternative models are needed for data-poor situations and to allow for quicker response times. Such is the case for the market squid (*Loligo opalescens*) fishery off the western United States.

In California waters, the market squid has become the largest fishery in terms of both tonnage landed and monetary value (Vojkovich 1998; California Department of Fish and Game (CDFG) 2002). The increased pressure on this species has led resource managers, scientists, and fishermen to attempt to estimate sustainable fishing levels (Department of Commerce 1998; Pacific Fishery Management Council 1998). Management efforts have been hampered by the lack of rigorous measures of population abundance and fishing effort as well as uncertainty surrounding the nature of the spawner–recruit relationship.

More solid information exists for the reproductive physiology of female market squid. Importantly, independent studies indicate that female fecundity is fixed at sexual maturity (Knipe and Beeman 1978; Macewicz et al. 2004). This result allows one to assume that, on a per-female basis, egg production is a depletion process of an initial quantity of eggs. From this notion, we present a per-recruit model derived from classical yield-per-recruit and spawning stock biomass per recruit theory (Beverton and Holt 1957; Gabriel et al. 1989) that tracks the dynamics and fecundity of maturity cohorts (e.g., Beverton et al. 1994; Murawski et al. 2001). Our model's utility lies in its use of basic biometric data on female anatomy to infer fishing mortality rate and management reference points such as egg escapement and yield-per-recruit. This is in contrast with the typical use of yield-per-recruit models where a priori estimates of fishing mortality are required. Central to the formulation and implementation of our model is the notion of catch fecundity: the number of eggs remaining in the reproductive tracts of females captured by the fishery. The present model offers the additional advantage of delivering instantaneous calculations of egg escapement, should such information be desirable.

Materials and methods

Market squid fishery and biology

Market squid occur in the California and Alaska current systems along the coast of North America from the southern tip of Baja California to southeastern Alaska (Hixon 1983). Off central and southern California, much spawning occurs nearshore in shallow waters (Fields 1965; Hixon 1983). Spawning aggregations are dense with adults. Fishermen typically use light boats to attract and concentrate the squid near the surface and then deploy purse-seine nets to capture them (Vojkovich 1998). Nearly all of the squid taken by the fishery are sexually mature (CDFG 2001). Newly matured individuals appear to move onto the spawning aggregations on a continuous basis, and the average age of spawners is about 6 months (Butler et al. 1999; CDFG 2001; Jackson and Domeier 2003).

California market squid live less than 1 year and begin to reach sexual maturity 4 or 5 months after hatching (Jackson 1994; Butler et al. 1999; CDFG 2001). Recent work by Macewicz et al. (2004) confirms Knipe and Beeman's (1978) earlier indication that female market squid do not create new gametes after sexual maturation. In both studies, early oogonia were not found in the ovaries of mature females. Thus, market squid females can be classed as having "fixed" or "determinate" fecundity. Females may lay a large proportion of their eggs within the first few days following maturity (Macewicz et al. 2004). The length of the female's reproductive life span is not clear. Two cohorts of laboratory-reared market squid laid eggs for 50–60 days before their fecundity was exhausted; all squid were dead 10–20 days after the laying of the last egg capsule (Yang et al. 1986). In nature, where natural mortality is higher, it is likely that an individual female deposits eggs over a shorter period of time, possibly dying soon after her reproductive career (McGowan 1954).

Model summary

The model performs discrete-time per-recruit calculations for an initial cohort of immature female recruits using daily time steps. These immature females are assigned the age of 4 months posthatching; therefore, the dynamics of early life

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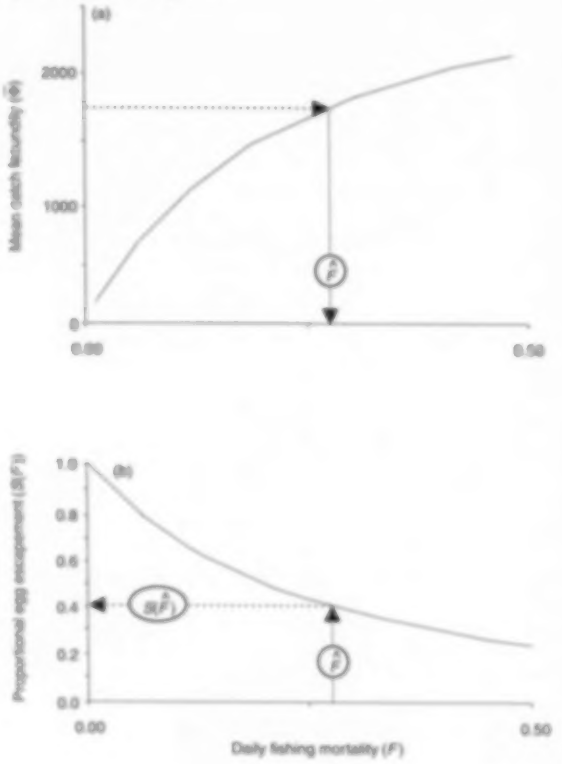
stages are not considered. Every day, a certain proportion of the immature females become sexually mature (i.e., a maturity cohort), with the remainder continuing somatic growth subject to natural mortality. Females of a maturity cohort have an initial number of eggs, determined by their mantle length at maturity. Each day, mature females lay eggs while subject to natural and fishing mortality. Thus, over time, each maturity cohort decreases in number while its surviving females deplete their initial number of eggs. The egg production of all maturity cohorts is summed to find spawned eggs-per-recruit and proportional egg escapement. For mature females that succumb to fishing mortality, the eggs remaining in their reproductive tracts are calculated (catch fecundity). The catch fecundity of captured females reflects the magnitude of fishing mortality and egg escapement. As fishing effort increases, mature females will be captured sooner in their reproductive careers, with many eggs remaining in their bodies. Therefore, catch fecundity increases as the rate of fishing mortality increases (Fig. 1*a*). At the same time, fewer eggs are actually spawned as fishing mortality increases, so egg output decreases with fishing mortality (Fig. 1*b*). Through these relationships, the model simultaneously calculates levels of yield and spawned eggs-per-recruit for an inferred rate of fishing mortality.

Fig. 1. Modeling approach. (*a*) Mean catch fecundity ($\bar{\Phi}$) increases as daily fishing mortality rate (F) increases. Mean catch fecundity is calculated for a sample of harvested females, and daily fishing mortality rate ($\hat{F}$) is inferred from the curve generated by the model. (*b*) Proportional egg escapement decreases as daily fishing mortality rate increases. This curve allows for calculation of proportional egg escapement ($S(\hat{F})$) from the inferred daily fishing mortality rate.



Growth and maturation

All immature females of the initial cohort start at the same age (t_{min}) (definitions and values for all parameters are given in Table 1). We set t_{min} = 120 days, which represents the age of the youngest mature female observed in the California fishery. Calculations are performed for ages up to t_{max} = 360 days, which is the maximum age reported for the market squid (Jackson 1994; Butler et al. 1999; CDFG 2001). Time steps (t) are daily, and age is measured in days.

For immature females, mantle length on day t (L_t^I, $t \geq 120$ days) is found by an exponential growth curve:

$$(1) \qquad L_t^I = \alpha e^{\beta t}$$

where α and β are parameters for market squid (Table 1). Female market squid may stop somatic growth in mantle length after sexual maturity (CDFG 2001), so model runs alternately assume that growth stops at maturity or that growth continues in mature females according to the growth equation for immature females (eq. 1). Body mass at age for individual immature squid is $B_t^I = \kappa(L_t^I)^\nabla$. For a mature squid, body mass at age is $B_t^m = \kappa(L_t^m)^\nabla$, where L_t^m is length on day t.

For modeling purposes, we posit a length-dependent maturation process, as opposed to age dependent. Several data sets indicate a maturation threshold of approximately 10 cm in dorsal mantle length for females (Butler et al. 1999; CDFG 2001; Jackson and Domeier 2003). That is, once females reach approximately 10 cm in mantle length, they appear to switch on maturity. Furthermore, mature females show a much tighter range in mantle length (approximately 10–15 cm) than in age (approximately 120–300+ days), which suggests a better-defined length criterion for maturity, rather than age.

For market squid, overall mortality rates are likely higher for mature than for immature females owing to the energetic demands, predation risks, and targeted fishing at the spawning grounds (McGowan 1954; Caddy 1996). Higher mortality for mature females would make a sample composed of immature and mature females skewed towards higher proportions of immature individuals, thereby artificially biasing estimates of maturity at length or age (Maki et al. 2002). We refine standard maturity at length relationships to calculate the daily probability that an immature female becomes mature (p_t). The probability p_t differs from the conventional probability that a randomly sampled female will be sexually mature. In particular, p_t will be higher than the fraction of mature individuals in a sample when mature individuals die faster than immature individuals.

If mature and immature females had the same mortality risk, then the proportion becoming mature on day t would be as conventionally described:

$$p_t = \frac{1}{1 + e^{-(\delta + \gamma L_t^I)}}$$

where δ and γ are parameters. In this circumstance, the proportion of immature females that do not mature is

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Table 1. Symbols used in the model.

	Units	Default value	Description
Notation			
a	—	—	Subscript to denote day of maturation for a group of females (i.e., maturity cohort a)
m, I	—	—	Superscripts to denote variables and parameters for mature and immature females, respectively
t	—	—	Subscript to denote age in days
Variable			
B_t^m, B_t^I	g	—	Body mass at age t for mature and immature females, respectively
$C_{a,t}^m, C_t^I$	Female	—	Number of mature females of maturity cohort a captured at age t, number of immature females captured at age t
$C_{\text{Total}}^m, C_{\text{Total}}^I$	Female	—	Total number of mature (or immature) females captured by the fishery
E_a	Eggs·female^{-1}	—	Potential fecundity for females of maturity cohort a
$E(F)$	Eggs·female^{-1}	—	Eggs laid per female recruit at fishing mortality rate F
$f_{a,t}$	Eggs	—	Eggs laid by maturity cohort a at age t
L_t^m, L_t^I	mm	—	Mantle length at age t for mature and immature females
$N_{a,t}^m, N_t^I$	Female	—	Number of mature females of maturity cohort a at age t, number of immature females at age t
p_t	na	—	Daily proportion of immature females that become mature at age t assuming equal mortality risk for immature and mature females
$r_{a,t}$	Eggs·female^{-1}	—	Residual fecundity for a female in maturity cohort a at age t
$R_{a,t}$	Eggs	—	Residual fecundity for entire maturity cohort a at age t
$S(F)$	na	—	Proportional egg escapement; eggs laid per female recruit, relative to maximum value, at fishing mortality rate F
u_t	na	—	Proportion of immature females that do not reach sexual maturity at age t
$W_{a,t}^m, W_t^I$	g	—	Total body mass of maturity cohort a (or immature females) captured at age t
W_{Total}	g	—	Total body mass for all females captured by the fishery
$Y(F)$	g·female^{-1}	—	Yield (in biomass) per female recruit at fishing mortality rate F
Δ_t	na	—	Proportion of immature females that reach sexual maturity at age t
$\varepsilon_{a,t}$	Eggs	—	Eggs taken by the fishery of maturity cohort a at age t
$\theta_{a,t}$	na	—	Standardized catch fecundity for a female of maturity cohort a captured at age t
$\bar{\theta}$	na	—	Mean standardized catch fecundity calculated over all maturity cohorts
$\xi_\varphi, \xi_\varphi'$	na	—	Values calculated in sensitivity analyses with default and 10%-modified parameter values, respectively
$\Phi_{a,t}$	Eggs·female^{-1}	—	Catch fecundity (number of eggs in the reproductive tract of a female of maturity cohort a captured at age t)
$\bar{\Phi}$	Eggs·female^{-1}	—	Mean catch fecundity calculated over all maturity cohorts
Parameter			
F	day^{-1}	Varies	Instantaneous daily fishing mortality rate for mature females
M^m, M^I	day^{-1}	Varies, 0.01	Instantaneous daily natural mortality rate for mature and immature females, respectively
s	na	0	Vulnerability of immature females to fishing gear relative to mature females
$t_{\min}$	days	120	Initial age of all females in the model
$t_{\max}$	days	360	Maximum age
ν	day^{-1}	Varies	Instantaneous daily rate of egg laying
$\bar{X}$	day^{-1}	—	Total instantaneous daily rate of egg removal from spawning population owing to egg laying, natural mortality, and fishing mortality
Z	day^{-1}	—	Sum of instantaneous daily natural and fishing mortality rates

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Table 1 (*concluded*).

	Units	Default value	Description
α	mm	3	Length–age parameter
β	day^{-1}	0.019	Length–age parameter
γ	mm^{-1}	0.158	Maturity–length parameter
δ	na	−15.46	Maturity–length parameter
κ	g·mm^{-1}	0.00027	Length – body mass parameter
λ	Eggs·mm^{-1}·female^{-1}	29.8	Potential fecundity parameter
ψ	na	2.47	Length – body mass parameter

$$(2)\qquad u_t = 1 - p_t = 1 - \frac{1}{1 + e^{-(\delta+\gamma L_t^1)}} = \frac{e^{-(\delta+\gamma L_t^1)}}{1 + e^{-(\delta+\gamma L_t^1)}}$$

Considering only immature squid of the same size and mortality risk, the daily proportion that becomes sexually mature is

$$(3)\qquad \Delta_t = \frac{u_{t-1} - u_t}{u_{t-1}}$$

For simplicity, and because Δ_t approaches 1.0 asymptotically, we assume that maturation precedes mortality events on each day and that all females are mature by age 270 days (i.e., $\Delta_{270} = 1$). For age $t_{max} - 1$, the rate of maturation is $\Delta_t = 1 - u_t$.

For modeling purposes, maturity parameters δ and γ for market squid were estimated by fitting a conventional logistic curve of maturity at length data from survey samples (CDFG 2001). Thus, the estimated maturity parameters are probably biased. Although these estimates are crude and remain uncertain, the reformulated eqs. 2 and 3 are a more realistic approach to calculate sexual maturity for market squid.

Population dynamics

The number of immature females (N_t^1) at the beginning of each day is

$$(4)\qquad N_t^1 = (1 - \Delta_t) N_{t-1}^1 e^{-M^1 - sF}$$

where M^1 is the natural mortality rate for immature squid, s is the vulnerability of immature squid to the fishing gear relative to mature squid ($0 \le s \le 1$), and F is the daily fishing mortality rate for mature females. The initial number of immature females, $N_{t_{min}}^1$, is arbitrarily set to 1000. In most runs, $s = 0$ because landings are nearly 100% mature squid (CDFG 2001; Jackson and Domeier 2003).

We track abundance of mature squid $N_{a,t}^m$ in terms of daily maturity cohorts. A maturity cohort is defined as a group of females that mature on a certain day a. The initial number of females in maturity cohort a is

$$(5)\qquad N_{a,t=a}^m = \Delta_t N_{t-1}^1 e^{-M^1 - sF}$$

where $N_{t-1}^1 e^{-M^1 - sF}$ is the number of immature individuals alive at the end of day $t = a - 1$ and just before the individuals that comprise maturity cohort a become sexually mature. Subsequent abundance of the maturity cohort is

$$(6)\qquad N_{a,t+1}^m = N_{a,t|a} e^{-M^m - F}$$

where M^m is the daily natural mortality rate for mature squid ($M^m >> M^1$). Mature females of all sizes and ages are assumed to be equally vulnerable to fishing mortality during each day of the remainder of their lives.

The number of mature females of maturity cohort a captured on day t is

$$(7)\qquad C_{a,t}^m = N_{a,t}^m \frac{F}{M^m + F}(1 - e^{-M^m - F})$$

In units of mass, the catch of mature females is

$$(8)\qquad W_{a,t}^m = C_{a,t}^m (\kappa (L_t^m)^\psi)$$

In model runs where immature squid are vulnerable to fishing gear ($s > 0$), the numbers (C_t^1) and biomass (W_t^1) of captured immature squid are calculated by substituting parameters and variables for immature squid in eqs. 7 and 8. Importantly, the product sF replaces F in eq. 7. Total catch (W_{Total}) is found by summing the catches of mature and immature squid.

Fecundity and egg production

Following Macewicz et al. (2004), "potential fecundity" is the number of viable gametes in a newly mature female's reproductive tract. For simplicity, we call all gametes in a female's reproductive tract eggs, regardless of whether they occur in the ovary or oviduct. Under the assumption of fixed fecundity at maturation, potential fecundity is the female's total reservoir of eggs at sexual maturity. From Macewicz et al. (2004), potential fecundity for females that mature on day a (E_a) is a function of their mantle length on this day (L_a^1):

$$(9)\qquad E_a = \lambda L_a^1$$

where λ is a parameter (Table 1).

Once reaching sexual maturity, females are assumed to lay eggs continuously at a constant daily rate (v). We define residual fecundity as the number of eggs in a mature female's reproductive tract after some spawning activity. At the beginning of a given day t, residual fecundity for females that matured on day a is

$$(10)\qquad r_{a,t} = E_a e^{-v(t-a)}$$

We assume that egg laying and natural and fishing mortality occur simultaneously because disruption of an individual's egg laying by predators or fishing gear is possible on the harvested spawning grounds.

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For modeling, it is useful to calculate the total number of eggs in the reproductive tracts of all females in each maturity cohort at the beginning of a given day t:

$$R_{a,t} = N^{m}_{a,t} r_{a,t} \quad (11)$$

The number of eggs actually spawned during a given day t by a maturity cohort, $f_{a,t}$, is the number removed from the females' reproductive tracts due to spawning, considering simultaneous losses to fishing and natural mortality:

$$f_{a,t} = R_{a,t} \frac{v}{X}(1 - e^{-X}) \quad (12)$$

where $X = v + F + M^{m}$ is the total daily instantaneous rate at which eggs are removed from the spawning population due to all causes.

Females taken by the fishery during day t will have spawned some eggs, making their catch fecundity (the number of eggs in their reproductive tracts at capture) less than $r_{a,t}$. Taking into account losses due to natural mortality and spawning, the total number of eggs taken by the fishery from a maturity cohort during a given day t is

$$\varepsilon_{a,t} = R_{a,t} \frac{F}{X}(1 - e^{-X}) \quad (13)$$

On a per-female basis, catch fecundity for a female captured on day t is

$$\Phi_{a,t} = \frac{\varepsilon_{a,t}}{C^{m}_{a,t}} = \frac{R_{a,t} \frac{F}{X}(1 - e^{-X})}{N^{m}_{a,t} \frac{F}{Z}(1 - e^{-Z})} = \frac{N^{m}_{a,t} r_{a,t} \frac{F}{X}(1 - e^{-X})}{N^{m}_{a,t} \frac{F}{Z}(1 - e^{-Z})} = \frac{r_{a,t} Z(1 - e^{-X})}{X(1 - e^{-Z})} \quad (14)$$

where Z is the total daily instantaneous mortality rate for mature females (i.e., $Z = F + M^{m}$) and $C^{m}_{a,t}$ is the number of females of maturity cohort a captured on day t.

Macewicz et al. (2004) compute "standardized" catch fecundity for females. Standardized catch fecundity expresses a female's catch fecundity as a fraction of her potential fecundity. In our model, all females within a maturity cohort follow the same reproductive schedule, so standardized catch fecundity ($\theta_{a,t}$) for a female that matured on day a and was captured on day t is

$$\theta_{a,t} = \frac{\varepsilon_{a,t}/C^{m}_{a,t}}{E_a} = \frac{\Phi_{a,t}}{E_a} \quad (15)$$

Management reference points

Yield-per-recruit and spawned eggs-per-recruit are calculated by standard methods (Beverton and Holt 1957; Ricker 1975; Gabriel et al. 1989). Yield-per-recruit $Y(F)$ at a particular fishing mortality rate F is the total catch in biomass divided by the initial number of immature female recruits:

$$Y(F) = \frac{W_{\text{Total}}}{N^{I}_{t_{\min}}} = \frac{\sum_{t=t_{\min}}^{t_{\max}} W^{I}_{t} + \sum_{t=t_{\min}}^{t_{\max}} \sum_{a=t}^{t_{\max}} W^{m}_{a,t}}{N^{I}_{t_{\min}}} \quad (16)$$

Similarly, the number of spawned eggs-per-recruit at a particular fishing mortality rate $E(F)$ is

$$E(F) = \frac{\sum_{t=t_{\min}}^{t_{\max}} \sum_{a=t}^{t_{\max}} f_{a,t}}{N^{I}_{t_{\min}}} \quad (17)$$

Our calculation of spawned eggs-per-recruit is a specific case of Mace and Sissenwine's (1993) "spawning unit per recruit" (SPR). In our model, we have defined the spawning unit as a spawned egg. Spawned eggs-per-recruit is maximal at $F = 0$, so proportional egg escapement $S(F)$ at a fishing mortality rate greater than zero ($F > 0$) is

$$S(F) = \frac{E(F > 0)}{E(F = 0)} \quad (18)$$

Our definition of proportional egg escapement is consistent with the usage in Macewicz et al. (2004) and is analogous to Mace and Sissenwine's (1993) "percent spawning per recruit" (%SPR) and Goodyear's (1993) "spawning potential ratio" (SPR).

For all maturity cohorts, the mean catch fecundity, or the mean number of eggs remaining in the reproductive tracts of females captured by the fishery, is

$$\overline{\Phi} = \frac{\sum_{t=t_{\min}}^{t_{\max}} \sum_{a=t}^{t_{\max}} \varepsilon_{a,t}}{C^{m}_{\text{Total}}} \quad (19)$$

where the total number of mature females caught is

$$C^{m}_{\text{Total}} = \sum_{t=t_{\min}}^{t_{\max}} \sum_{a=t}^{t_{\max}} C^{m}_{a,t}$$

Alternatively, mean catch fecundity can be calculated as the catch-weighted sum of daily catch fecundity for each maturity cohort:

$$\overline{\Phi} = \frac{\sum_{t=t_{\min}}^{t_{\max}} \sum_{a=t}^{t_{\max}} \Phi_{a,t} C^{m}_{a,t}}{C^{m}_{\text{Total}}} \quad (20)$$

Similarly, mean standardized catch fecundity is

$$\overline{\theta} = \frac{\sum_{t=t_{\min}}^{t_{\max}} \sum_{a=t}^{t_{\max}} \theta_{a,t} C^{m}_{a,t}}{C^{m}_{\text{Total}}} \quad (21)$$

Model scenarios

The model's default scenario used the best current estimate for each parameter (Table 1). Our initial analysis explored the model's behavior under a range of values for mature natural mortality rate (M^{m}) and egg laying rate (v). Natural mortality rate for mature females was 0.01, 0.15, or 0.45·day^{-1}. This range encompasses estimates of M = 0.3·month^{-1} (or 0.01·day^{-1}) for other *Loligo* spp. (Brodziak 1998; Agnew et al. 1998) and higher mortality rates suggested for *L. opalescens* (Macewicz et al. 2004). Egg laying

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rate was either 0.45 or 0.225·day^{-1}. The value v = 0.45·day^{-1} was the best estimate assuming that a female spawned 36% of her potential fecundity immediately (during the first day) after sexual maturity; i.e., $(1.00 - 0.36) = e^{-0.45}$ (Macewicz et al. 2004). The alternative v = 0.225·day^{-1} was chosen to examine lower rates of egg laying. We systematically varied daily fishing mortality rate (F) from 0.0 to 1.0·day^{-1} for each combination of values for M^m and v.

For each combination of the above parameter values, we assumed that growth in mantle length either continued or stopped at sexual maturity. For either case, a female's potential fecundity (E_o) was calculated and fixed on the day of maturity. Natural mortality for immature females was set at M^i = 0.01·day^{-1}. Values for other parameters, such as those for maturity and length at age (i.e., δ, γ, α, β, etc.), were taken from ongoing analyses.

We performed a second set of sensitivity analyses by systematically varying mature natural mortality (M^m), egg laying rate (v), vulnerability of immature squid to fishing (s), and maturity parameters (δ and γ). We set default values for this suite of parameters (Table 1) and then varied each parameter value by 10% in the direction of increased spawned eggs-per-recruit. In this set of runs, we set the default value of immature vulnerability (s) to 0.02, rather than zero, to allow for a decrease in this parameter, which is in the direction of increased eggs-per-recruit. The sensitivity of each management reference point was quantified as percent change (i.e., $100\% \times (\xi^{s'} - \xi)/\xi$), where $\xi^{s'}$ and ξ were the reference point values calculated with the 10%-modified and default parameter values, respectively.

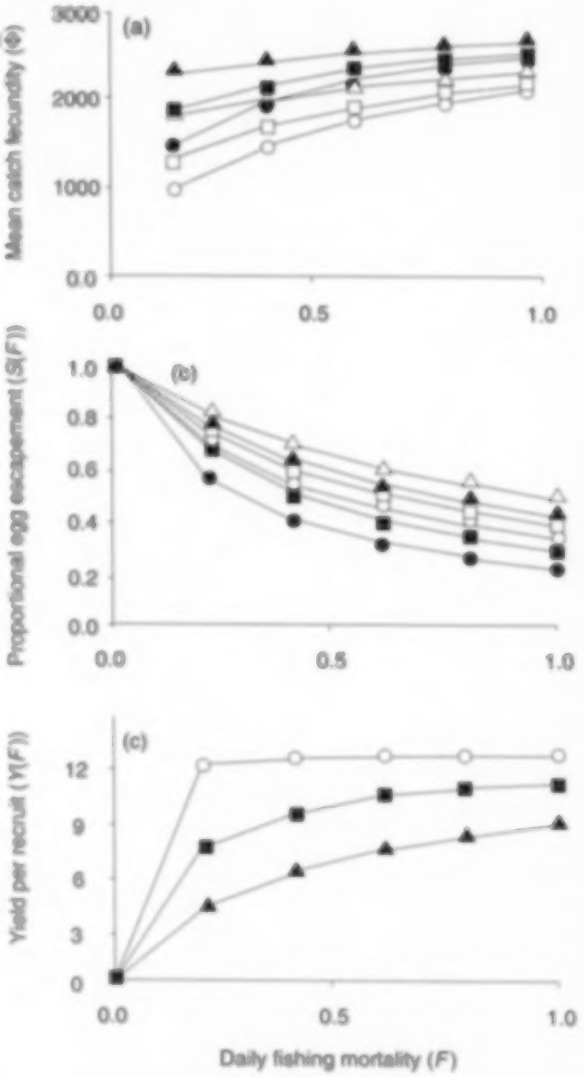
Results

The initial exploration of natural mortality (M^m) and egg laying rates (v) demonstrates that increasing natural and fishing mortality rates lead to increasing mean catch fecundity (Fig. 2*a*). Similarly, decreasing the egg laying rate increased the mean catch fecundity. Standardized catch fecundity showed qualitatively identical patterns.

Proportional egg escapement decreased with fishing mortality but increased as egg laying rate increased (Fig. 2*b*). Somewhat paradoxically, egg escapement is higher when the rate of natural mortality increases (Fig. 3*a*). This result occurred because proportional egg escapement is spawned eggs-per-recruit relative to the maximum value under the particular combination of biological parameters. At a high natural mortality rate, such as M^m = 0.45, the maximum eggs-per-recruit is about 800 (Fig. 3*b*). Increasing fishing mortality lowers eggs-per-recruit, but it is not a large proportional decrease in this case. In contrast, low natural mortality (say M^m = 0.01) results in a larger maximum eggs-per-recruit value (Fig. 3*b*). In this case, increasing fishing mortality produces steeper proportional declines in eggs-per-recruit.

Yield-per-recruit increased asymptotically with fishing mortality and decreased as natural mortality increased (Fig. 2*c*). Yield-per-recruit was independent of egg laying rate. The results presented in Fig. 2 were obtained by assuming no mantle growth after sexual maturity. Results are very robust to this assumption. When mantle growth was allowed to continue after maturity, a substantial quantitative difference was seen only for yield-per-recruit with low natural mortality (M^m = 0.01). In this case, yield-per-recruit increased to 14 for low values of fishing mortality but decreased to approxomately 12 by F = 1 (as in Fig. 2*c*).

Fig. 2. Model response to combinations of daily natural mortality rate for mature females (M^m) and egg-laying rate (v). All other parameters have default values. (*a*) Mean catch fecundity; (*b*) proportional egg escapement; (*c*) yield-per-recruit. ●, M^m = 0.01, v = 0.225; ○, M^m = 0.01, v = 0.450; ■, M^m = 0.15, v = 0.225; □, M^m = 0.15, v = 0.450; ▲, M^m = 0.45, v = 0.225; △, M^m = 0.45, v = 0.450.



Changes in reference points following a 10% change to default parameter values reveal substantial effects of decreasing immature gear vulnerability (s) on spawned eggs-per-recruit and proportional egg escapement (Table 2). Decreasing the gear vulnerability of immature squid allowed more squid to reach sexual maturity, thereby increasing egg output by the entire cohort. This effect was stronger when

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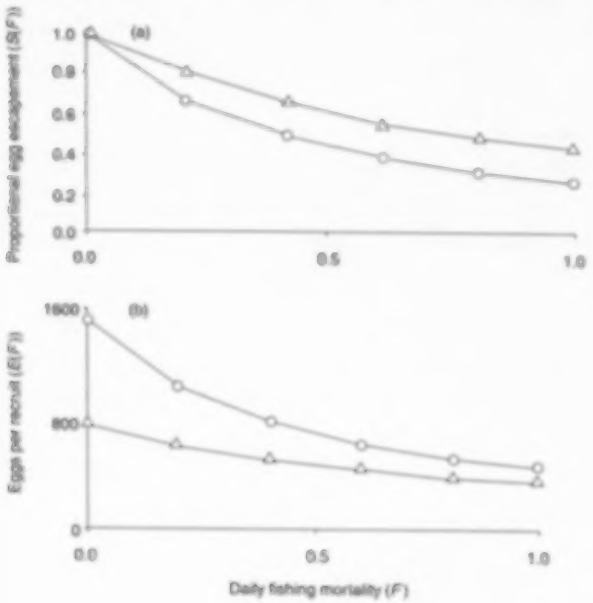
Fig. 3. Effect of daily natural mortality rate for mature females (M^m) on measures of reproductive output. △, $M^m = 0.45$; ○, $M^m = 0.01$. (*a*) Proportional egg escapement; (*b*) spawned eggs-per-recruit.



fishing mortality was increased to very high levels (i.e., $F = 1$ and $F = 2$), where the effects on spawned eggs-per-recruit and egg escapement were increased by factors of 2–4. Thus, as overall fishing mortality increases, decreasing the vulnerability of immature squid to the fishing gear greatly increases the population's reproductive output.

Changes to the maturity parameters (δ and λ) increased the rate of sexual maturation (Table 2). This enabled immature females to reach maturity at earlier ages. The increased influx of mature females increased proportional egg escapement. At higher levels of fishing mortality ($F = 1$ and $F = 2$), the effects on spawned eggs-per-recruit and proportional egg escapement increased by factors of 4–20. Increasing the rate of sexual maturity has the added effect of decreasing length at maturity. Shorter length at maturity results in strongly reduced yield-per-recruit (Table 2). Shorter length at maturity also leads to lower potential fecundity, which results in lower values of catch fecundity (Table 2). Standardized catch fecundity was unaffected by changes in the maturity parameters.

Discussion

Mortality rates affect many of the model's results. Spawned eggs-per-recruit decreases as fishing or natural mortality rates increase, while mean catch fecundity increases as either rate increases. Both patterns result from females failing to lay many eggs under high mortality rates. Proportional egg escapement decreases as fishing mortality increases while actually increasing as natural mortality increases. The latter trend is somewhat counterintuitive and is explained by relatively smaller decreases in spawned eggs-per-recruit relative to the maximum attainable as natural mortality increases. Yield-per-recruit increases asymptotically with fishing mortality but decreases with natural mortality. With regard to the rate of egg laying, increasing this rate increased spawned eggs-per-recruit while decreasing catch fecundity.

The model was largely insensitive to the assumption of cessation of mantle growth after sexual maturity. Relaxing this assumption showed a slight increase in yield-per-recruit only at combinations of low fishing and low natural mortality rates. Under such a regime of low overall mortality, a mature female can live long enough to attain a mantle length that is significantly longer than that at maturity. This scenario seems improbable for loliginid squid, however, because females are likely to experience accelerated mortality rates upon maturation and reproduction (McGowan 1954; Caddy 1996). Furthermore, the energetics of reproduction may constrain somatic growth in many loliginid squid (Moltschaniwskyj 1995; Moltschaniwskyj and Semmens 2000; Jackson and Moltschaniwskyj 2002). In the model, the occurrence of mantle growth does not affect the asymptotic behavior of yield-per-recruit as fishing mortality increases.

Parameters that apply to the immature females, such as gear vulnerability (s) and maturity rate (δ and λ), have large effects on catch fecundity, proportional egg escapement, and yield-per-recruit. Changing the rates of capture and maturity for immature females greatly affects the number of females that reach sexual maturity, thereby affecting egg escapement and yield-per-recruit. These parameters also influence length at maturity. Length at maturity determines eggs at maturity (i.e., potential fecundity), but it does not affect how quickly the eggs are laid. Thus, two females can have different numbers of eggs at maturity but will lay them at the same relative rate. Upon capture, they will have different catch fecundities in terms of eggs in body at capture, but their standardized catch fecundities (i.e., ratio of eggs at capture to eggs at maturity) will be the same. This subtle, but important, difference is seen in the effect of immature vulnerability and maturation rate on mean catch fecundity but not on mean standardized catch fecundity. In real practice, both forms of catch fecundity should be calculated. A change in absolute catch fecundity accompanied by a lack of change in the standardized form could indicate fundamental changes in fishery operations or developmental conditions for the squid.

The model's response to parameters for the immature females highlights an important point. Increased fishing mortality on immature females is expected to decrease proportional egg escapement, and this decrease will be greater than the gain in yield-per-recruit. It is therefore imperative to monitor catches for immature females. A sampling program that estimates catch fecundity for mature females while ignoring the presence of immature females runs the risk of detecting immature fishing mortality rather slowly while overestimating egg escapement.

An approach for management of market squid

This per-recruit approach offers advantages for management of the market squid fishery. First, the model is rooted in basic data that are collected on females in the catch. In the simplest scenario, captured females would be randomly sampled during the fishing season. For each female, catch

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Table 2. Sensitivity of management reference points to changes of parameter values by 10% of default values.

Parameter changed	Mean catch fecundity $\bar{\Phi}$	Mean standardized catch fecundity $\bar{\theta}$	Yield-per-recruit $Y(F)$	Eggs-per-recruit $E(F)$	Proportional egg escapement $S(F)$
Natural mortality rate M^m	–1.0	–1.0	1.8	1.4	–1.0
Egg-laying rate ν	–3.9	–3.9	0	5.7	3.5
Immature gear vulnerability s	0.1	0	3.1	6.6	6.6
Maturity–length parameter δ	–10.4	0	–14.7	0.6	5.9
Maturity–length parameter λ	–9.2	0	–13.5	0.5	5.6

Note: Default parameter values for this analysis: $M^m = 0.15$, $\nu = 0.45$, $s = 0.02$, $\delta = -15.46$, and $\lambda = 0.158$. Values in the table represent the effect on reference points, i.e., effect = $100\% \times (\xi_i^* - \xi_i)/\xi_i$, where ξ_i^* and ξ_i are the reference point values calculated with the 10%-modified and default parameter values, respectively. In this analysis, $F = 0.5$.

fecundity ($\Phi_{a,\ell}$) would be calculated directly by counting the number of eggs in her reproductive tract or indirectly through biometric proxies such as mantle thickness and gonad mass (Macewicz et al. 2004). To calculate a female's standardized catch fecundity, we can use her mantle length to estimate her potential fecundity ($E_{a,\ell}$), as in Macewicz et al. (2004). A mean value of catch fecundity, with some measure of variation, is then calculated for the sampled females.

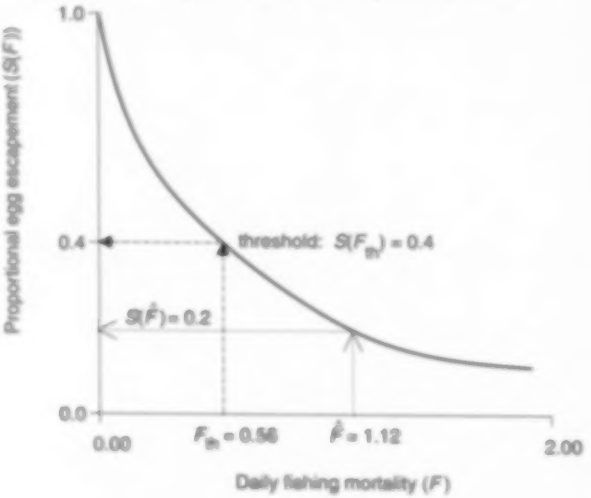
Second, the present model does not require an outside stock assessment model to estimate fishing mortality. Fishing mortality along with spawned eggs-per-recruit, proportional egg escapement, and yield-per-recruit are inferred from mean catch fecundity. This allows for stock management wherein the calculated egg escapement is checked against a threshold value. Should egg escapement fall below this threshold, the response curve of egg escapement to fishing mortality indicates the required degree of fishing reduction to bring escapement back to the threshold level (Fig. 4).

We note that certain issues need to be addressed before implementing the present model in management. First, values of fishing mortality rate will be inferred with some uncertainty owing to variation in the estimated mean catch fecundity, uncertainties in the model's parameters, and uncertainties concerning the model's structure and assumptions. Although we did not evaluate the statistical properties of inferred fishing mortality rates, short-cut approaches, such as deriving upper and lower bounds based on a range or confidence interval calculated for mean catch fecundity, can provide some measure of uncertainty surrounding fishing mortality. The present model offers a framework for more refined statistical calculations of fishing mortality, such as simulation, meta-analysis, or Bayesian approaches (Restrepo and Fox 1988; Dorn 2002).

Another issue is that, in actual practice, fishing mortality rate (F) must be translated into a real-world measure of effort (f), such as number of fishing nights or number of boats in operation. Positing a relationship such as $F = qf$ (where q is the catchability coefficient) enables one to scale fishing effort up or down to reach a desired egg escapement level. Ideally, a time series of inferred fishing mortality and measured fishing effort will elucidate the relationship between the two parameters.

A third issue is the formulation of a program to estimate catch fecundity from females captured by the fishery. At present, it is not clear how frequently to sample females from the fishery during the fishing season. For the market squid fishery off southern California, variability in somatic growth rate and fishing effort is evident between fishing seasons (Jackson and Domeier 2003; Maxwell et al. 2004). Within a fishing season, the squid experience several months of intense fishing pressure (Butler et al. 1999). In the initial stages of management, it may be best to err on the side of sampling the fishery too frequently so as to detect temporal changes in fishing mortality and in the females' reproductive physiology.

Fig. 4. Hypothetical management scenario. Suppose that the inferred daily fishing mortality rate for a stock is $\hat{F} = 1.12$, which corresponds to a proportional egg escapement of $S(\hat{F}) = 0.2$. In this case, egg escapement is below the a priori threshold escapement value of $S(F_{th}) = 0.4$. Fishing mortality would have to be reduced by one half to bring it to 0.56, which is the fishing mortality rate that corresponds to the 0.4 escapement threshold.



We note that, for simplicity, we assumed steady state for population age structure and parameter values in the present model. Such equilibrium assumptions are widely used in data-limited situations, with considerable success (Pauly and Morgan 1987). Preliminary demographic data on the market squid indicate monthly recruitment into the spawning population off southern California (CDFG 2001; Jackson and Domeier 2003). Although this result lends some support to steady-state assumptions, it most strongly points to the need for replicated demographic and biometric data within and between fishing seasons.

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Uncertainties and future research

Uncertainty is inherent in population modeling and stock assessment (Hilborn and Walters 1992; Ludwig et al. 1993). We acknowledge that many of the present model's biological parameters were imprecisely estimated. Although we addressed parameter uncertainty through sensitivity analyses, stock assessment requires much tighter ranges of parameter values than those explored in this model. Thus, future research should be devoted to reducing the plausible ranges of parameter values. For example, data on age, bioenergetic models of egg deposition, and observations of movement patterns to and from spawning sites will contribute towards the estimation of rates of natural mortality and egg laying.

For management, it would be useful to clarify relationships between proportional egg escapement and maximum sustainable yield (MSY) based biological reference points because fishery management agencies are typically guided by maximum sustainable yield concepts (e.g., Department of Commerce 1998). Fishing mortality rates near $F_{40\%}$ approximate F_{MSY} for some groundfish species (Clark 1991). Although comparable research has not been carried out for invertebrates, other squid fisheries have adopted an escapement threshold of $F_{40\%}$ (Beddington et al. 1990; Basson et al. 1996; Agnew et al. 1998). These values may serve as templates for squid management in the absence of analysis on particular stocks.

Finally, Hatfield and Des Clers (1998) raised the important issue of management based on absolute egg production rather than proportional egg escapement. Population persistence hinges upon the actual numbers of eggs spawned in the environment, regardless of whether each female laid 10% or 100% of her potential fecundity. For market squid, it would be advantageous to develop data collection programs and models that permit calculation of absolute egg production. One can also question whether the egg is the appropriate unit of escapement. Not all zygotes may hatch owing to biological factors such as unequal oxygen availability within the communal egg beds of loliginid squids and to fishery-related factors such as damage or removal of eggs by gear. After hatching, density-dependent effects such as competition and cannibalism within and between life stages can act to loosen the relationship between hatchling number and adult number as well as between adult number and egg number (Agnew et al. 2000). Managers of squid fisheries should be mindful of the tortuous path from zygote to adult and the potential interaction between population abundance and egg production.

Acknowledgements

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Food partitioning within the species-rich benthic fish community of Lake Malawi, East Africa

F. Duponchelle, A.J. Ribbink, A. Msukwa, J. Mafuka, D. Mandere, and H. Bootsma

Abstract: Temporal diet patterns were studied for nine species of haplochromine cichlids in Lake Malawi, East Africa, using a combination of stable isotope and stomach content analyses. The results illustrate the complementarity of the two approaches in elucidating dietary differences. Evidence was found that benthic algal production contributed to the energy requirements of offshore fishes that occupy depths between 10 and 30 m. The importance of the lake fly *Chaoborus edulis* as a food source for demersal fishes was confirmed, supporting the recent hypothesis that deep demersal fish production is principally sustained through the pelagic food chain rather than from benthic detrital sources. Isotopic differences were observed among species with apparently similar diets, feeding behavior, and depth preferences, suggesting that important resource partitioning exists among Lake Malawi benthic haplochromine cichlids.

Résumé : Les variations temporelles de régime alimentaire de neuf espèces de cichlidés haplochromis du lac Malawi (Afrique de l'est) ont été étudiées grâce à l'utilisation combinée des contenus stomacaux et des analyses d'isotopes stables. Les résultats illustrent la complémentarité des deux approches pour élucider les différences d'alimentation entre espèces proches. Cette étude a mis en évidence la contribution de la production algale benthique aux besoins alimentaires des poissons entre 10 et 30 m de profondeur. L'importance de *Chaoborus edulis* comme source alimentaire pour les espèces démersales a été confirmée, ce qui renforce l'hypothèse récente selon laquelle la production de poissons démersaux repose principalement sur une chaîne alimentaire de type pélagique et non pas sur des sources de détritus benthiques. Des stratégies trophiques distinctes ont été observées entre espèces ayant apparemment des préférences bathymétriques, des régimes et des comportements alimentaires similaires, ce qui suggère l'existence d'un important partage des ressources au sein des cichlidés haplochromis benthiques du lac Malawi.

Introduction

The Cichlid fishes have evolved an astonishing diversity of feeding adaptations and behaviours that enable them to utilize a large variety of food types, including phytoplankton, epilithic and epiphytic algae, plants, detritus, zooplankton, molluscs, insects, benthic invertebrates, fish eggs, larvae, scales, and whole fish (reviews in Fryer and Iles 1972; Ribbink 1990; Yamaoka 1991). The role of the feeding apparatus and trophic specializations in the adaptive radiation of African cichlids has received much attention (Liem 1980, 1991; Ribbink et al. 1983). Many species appear to have diets that are nearly indistinguishable based on stomach content analyses (Greenwood 1981), raising uncertainties about the significance of neurocranial structure. McKaye and Marsh (1983) suggested that trophic partitioning might only be invoked when food resources are scarce. A number of studies in Lake Malawi (Reinthal 1990; Bootsma et al. 1996; Kuusipalo and Kakela 2000), Lake Tanganyika (Sturmbauer et al. 1992), and Lake Victoria (Bouton et al. 1997) have demonstrated the potential importance of trophic segregation, but mechanisms other than food resource partitioning may also allow for species coexistence (Genner et al. 1999*a*, 1999*b*, 1999*c*).

While diet, feeding behaviour, and trophic specializations in the nearshore rock-dwelling communities have received much attention, very little is known of the diverse offshore (sensu; Turner 1996) cichlid communities. Apart from the zooplanktivorous *utaka* group (*Copadichromis* spp.; Fryer and Iles 1972), the *chambo* group (*Oreochromis* spp.; Turner et al. 1991), and the pelagic species, whose feeding ecology was recently studied (Allison et al. 1996*a*; Ngatunga and

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F. Duponchelle,[1,2] A.J. Ribbink,[3] A. Msukwa, J. Mafuka, D. Mandere,[4] and H. Bootsma.[5] SADC/GEF, Lake Malawi Biodiversity Conservation Project, P.O. Box 311 Salima, Malawi.

[1]Corresponding author (e-mail: fabrice.duponchelle@ird.fr).
[2]Present address: IRD (UR 175) – GAMET, 362 rue JF Breton, BP 5095, 34033 Montpellier Cedex 1, France.
[3]Present address: JLB Smith Institute of Ichthyology, P Bag 1015, Grahamstown 6140 South Africa.
[4]Present address: Fisheries Research Unit, P.O. Box 27, Monkey Bay, Malawi.
[5]Present address: Great Lakes WATER Institute, University of Wisconsin-Milwaukee, 600 E. Greenfield Avenue, Milwaukee, WI 53204 USA.

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Allison 1996), the only information available on the diet of offshore fishes comes from Eccles and Trewavas (1989) and Turner (1996). These studies resulted in useful new insights into fish-feeding habits, but they were limited by the relatively small numbers of observations and the narrow time span over which fish stomach contents could be monitored. More recent studies in Lake Malawi have used stable isotope analysis to disentangle the trophic behavior of inshore (Bootsma et al. 1996) and rock-dwelling species (Genner et al. 1999*a*).

Both stomach content and stable isotope analyses have advantages and disadvantages that make them complementary. Stomach content analysis provides information about ingested food items over a very short time period, generally a few hours. Nevertheless, monitoring stomach content over long periods of time can give insights into seasonal or temporal trends in feeding patterns that may not be evident in stable isotope signatures because they represent a spatiotemporal integration of the assimilated food over periods varying from months to years, depending on fish growth rates and tissue turnover times (Peterson and Fry 1987; Hesslein et al. 1993; Gannes et al. 1997). Stable isotope signatures are useful when stomach contents cannot be identified, or when there is uncertainty regarding the assimilation efficiency of various food items. Stable isotope analysis is also useful for deep-water species that often have everted stomachs when retrieved from trawls.

In comparison with the structurally complex inshore zones (Ribbink et al. 1983; Konings 1995), offshore benthic zones are often poorly structured in Lake Malawi, and the typical substratum variability ranges from sand to mud (Konings 1995; Turner 1996; Duponchelle et al. 2003). Nevertheless, there are a number of potential food resources for cichlid fishes that occupy offshore habitats, including benthic invertebrates, zooplankton, sedimented phytoplankton, and other fish. Most offshore species studied to date seem to have a mixed diet made of varying proportions of these potential food items (Eccles and Trawavas 1989; Turner 1996). As a consequence, one might expect that the general trend of interspecific resource overlap often observed in inshore zones (McKaye and Marsh 1983; Ribbink et al. 1983; Genner et al. 1999*c*) might also occur, possibly to a larger extent, in the poorly structured offshore zones. The present study tests this hypothesis by investigating the temporal trends of some demersal fish diets using both monthly stomach content analysis and stable isotope analysis of carbon and nitrogen composition.

Material and methods

Fish sampling

Temporal variability of diet was determined over 8 months (November 1998 – May 1999) for nine demersal fish species that were selected according to their relative abundance and importance in the fishery. Each of these nine species is a dominant component of the fish community in its respective depth range (Duponchelle et al. 2003): *Lethrinops gossei*, *Lethrinops argenteus* (= *L. longipinnis* orange head), *Diplotaxodon limnothrissa*, *Diplotaxodon macrops*, *Copadichromis virginalis*, *Mylochromis anaphyrmus*, *Alticorpus mentale*, *Alticorpus macrocleithrum*, and *Taeniolethrinops praeorbitalis*. Fish were collected from monthly trawl surveys in the south-west arm (SWA) of Lake Malawi at depths of 10, 30, 50, 75, 100, and 125 m (see Duponchelle and Ribbink (2000) and Duponchelle et al. (2003) for details).

Stomach content analysis

During each monthly sampling event, 20 specimens of each species were sampled from the main catch as soon as the total catch weight was estimated. A solution of 15% formalin was injected into the abdominal cavity of each fish to ensure the preservation of food items, and the fish were fixed in a solution of 10% formalin for later examination. A problem frequently encountered when trawling below 50 m was that fish stomachs were everted during hauling. Every specimen from the whole catch of *A. mentale* was checked for intact stomachs, since the stomachs of these fish were almost always empty. Even apparently intact stomachs usually contained very little amounts of food.

When enough stomachs containing food items were available, five specimens of each species were analysed each month for diet composition. The method used was the modified version of the point method (Hynes 1950; Genner et al. 1999*a*). The weight of the stomach plus contents and the stomach minus contents were determined to the nearest 0.001 g. Total weight of stomach contents was calculated as the difference between the two weights. The stomach content was then examined under binocular microscope (10×–40× magnification) following the procedure detailed in Genner et al. (1999*c*).

Stable isotope analysis

Fish samples for stable isotope analysis were collected by trawling during the January 1999 cruise. Approximately six specimens of each of the nine target species, three small ones and three large ones whenever possible, were collected. Dorsal muscle tissue was subsampled for analysis. Potential food sources were collected during the April 1999 cruise. Gastropods and other benthic invertebrates were sorted out from grab samples taken at depths of 10, 30, 50, 75, 100, and 125 m. Sediment samples were taken from the upper layer (3 cm) of grab samples at every depth. Zooplankton and mayfly larvae were collected by 125-m vertical tows with a 50-µm mesh zooplankton net.

Stable isotope analyses were carried out with an isochrome continuous flow stable isotope mass spectrometer (Micromass; Waters Corp., Milford, Mass.) coupled to a Carlo Erba elemental analyzer (CHNS-O EA1108; ThermoFinnigan Italia S.p.A., Milan, Italy). Results were corrected to nitrogen standards IAEA-N1 and IAEA-N2 (both ammonium sulphate) and carbon standards IAEA-CH6 (sugar), EIL-72 (cellulose), and EIL-32 (graphite). EIL-70b, a lipid-extracted – ball-milled fish material, was used as a monitoring standard (EIL denotes internal standards, with values calculated using international standards). The error for clean ball-milled standard material was ±0.2‰ for carbon and ±0.3‰ for nitrogen. Standards were placed throughout each run at a range of weights to allow for additional linearity corrections, when necessary, for instrument fluctuations or samples of varying signal peak areas.

Statistical analyses

Interspecific differences in stable isotope signatures were analysed with an analysis of variance (ANOVA) and Tukey

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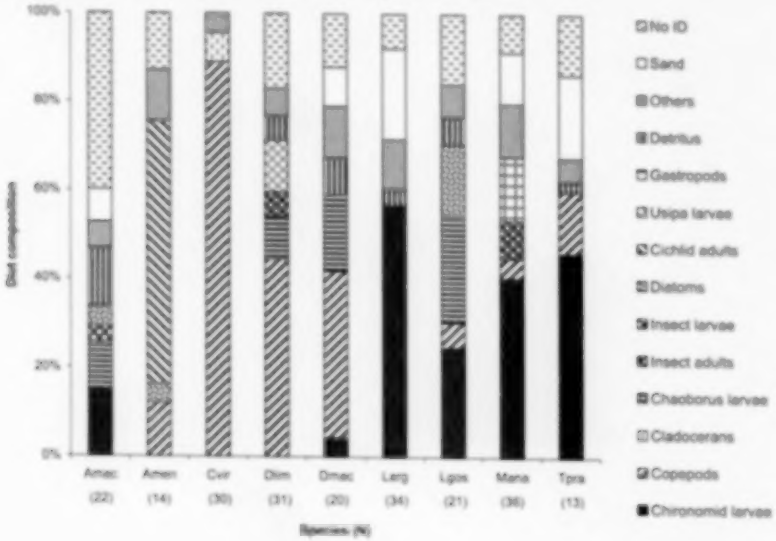
Fig. 1. Overall diet composition (% stomach content by weight) of nine demersal cichlid fishes in the SWA of Lake Malawi. Amac, *Alticorpus macrocleithrum*; Amen, *Alticorpus mentale*; Cvir, *Copadichromis virginalis*; Dlim, *Diplotaxodon limnothrissa*; Dmac, *D. macrops*; Larg, *Lethrinops argenteus*; Lgos, *L. gossei*; Mana, *Mylochromis anaphyrmus*; Tpra, *Taeniolethrinops praeorbitalis*. Items that made up less than 2% of the diet were lumped together and referred to as "Others". Unidentifiable materials were recorded as "No ID". "Detritus" refers to unidentifiable vegetal material and organic matter.



posthoc tests. Differences between small and large specimens within a species were assessed by regression analysis. All parametric tests were carried out after verifying the conditions of application.

The PRIMER 5 Package (Clarke and Warwick 1994) was used to analyse stomach content data following the procedure described in Genner et al. (1999*a*, 2003). A similarity matrix of the diet of the 221 individuals of the nine species was constructed using the Bray–Curtis similarity coefficient (Bray and Curtis 1957). Temporal differences of stomach content within and among species were analysed using the one-way ANOSIM (analysis of similarity) procedure on the similarity matrix. ANOSIM is a nonparametric test analogous to ANOVA. The test involves the calculation of a global test statistic R by contrasting the variance in similarity within groups with that between groups (Genner et al. 2003). Stomach content differences between small and large individuals (when small individuals with food in their stomach could be found (Appendix A)) were also tested with the one-way ANOSIM procedure.

Results and discussion

Diet analysis

There were significant differences in stomach content composition between every species pair except for *D. limnothrissa* and *D. macrops*, *L. argenteus* and *T. praeorbitalis*, and *M. anaphyrmus* and *T. praeorbitalis* (Fig. 1; Table 1). Except for *A. macrocleithrum*, *L. argenteus*, and *M. anaphyrmus*, there was significant intraspecific variability of either or both $\delta^{13}C$ and $\delta^{15}N$ for all species (Fig. 2). This was particularly striking for *A. mentale*, which covered $\delta^{13}C$ and $\delta^{15}N$ ranges of 3.75‰ and 3.05‰, respectively (Figs. 2*a* and 2*b*). For most of the species examined, this variability was mainly explained by size differences among individuals, confirming previous observations for the rock-dwelling species *Pseudotropheus callainos* (Genner et al. 2003). In general, smaller specimens had a lower $\delta^{15}N$ signature than larger ones, suggesting that they occupy a lower trophic level (Fig. 2*a*). However, *D. macrops*, *L. argenteus*, *L. gossei*, and *M. anaphyrmus* did not show significant variation of $\delta^{15}N$ with size, and *A. macrocleithrum* showed a decrease of $\delta^{15}N$ with size (Fig. 2*a*). Intraspecific variations of $\delta^{13}C$ also indicated that, for some species, small specimens fed on items that were different than the ones fed on by large ones (Fig. 2*b*). In *D. macrops*, *L. gossei*, and *T. praeorbitalis*, small specimens relied on food sources with heavier carbon signals than the ones relied on by larger specimens, whereas the opposite pattern was observed for *D. limnothrissa*. Small *L. argenteus* also tended to rely on food sources relatively enriched in carbon compared with those relied on by large specimens, but the differences were not significant. In *A. mentale*, *A. macrocleithrum*, *C. virginalis*, and *M. anaphyrmus*, there was no significant variation of $\delta^{13}C$ according to size. Because of these intraspecific variations in $\delta^{13}C$ and $\delta^{15}N$ ranges, small and large specimens of every species but *A. macrocleithrum*, *L. argenteus*, and *M. anaphyrmus* were subsequently separated in the interspecific analyses.

The average isotopic composition of the nine target species and their potential food sources are presented in Fig. 3. Owing to small sample size for most of the food sources, samples were analysed for $\delta^{13}C$ only, and few $\delta^{15}N$ measurements are available. The isotopic composition of adult mayflies is not displayed on this figure because, owing to their high mean $\delta^{15}N$ signature of 7.82, they are not likely to be a significant food source for these fish. The nine fish species displayed a total $\delta^{15}N$ range of 3.35‰. Although interspecific variance of $\delta^{15}N$ values may result from reliance on

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Table 1. Interspecific comparison of stomach content and stable isotope composition.

				Amen		Cvir		Dlim		Dmac			Lgos			Tpra	
			Amac	S	L	S	L	S	L	S	L	Larg	S	L	Mana	S	L
		$\delta^{13}C$															
Amen	S	$\delta^{13}C$															
		$\delta^{15}N$	**														
		St															
	L	$\delta^{13}C$	ns														
		$\delta^{15}N$	ns	**													
		St	**														
Cvir	S	$\delta^{13}C$															
		$\delta^{15}N$	**	ns	**												
		St															
	L	$\delta^{13}C$	ns		ns												
		$\delta^{15}N$	**	ns	**	ns											
		St	**		**												
Dlim	S	$\delta^{13}C$	ns		ns		ns										
		$\delta^{15}N$	**	ns	**	ns	ns										
		St															
	L	$\delta^{13}C$	**		ns		ns	ns									
		$\delta^{15}N$	ns	ns	ns	**	ns	*									
		St	**		**		**										
Dmac	S	$\delta^{13}C$	**		**		*	ns	ns								
		$\delta^{15}N$															
		St															
	L	$\delta^{13}C$	*		ns		ns	ns	ns	ns							
		$\delta^{15}N$	ns	**	ns	**	**	**	ns								
		St	**		**		**		ns								
Larg		$\delta^{13}C$	**		**		**	**	*	ns	**						
		$\delta^{15}N$	**	ns	**	*	ns	ns	ns		**						
		St	**		**		**		**		**						
Lgos	S	$\delta^{13}C$	**		ns		ns	ns	ns	ns	ns	*					
		$\delta^{15}N$															
		St															
	L	$\delta^{13}C$	ns		ns		ns	ns	ns	*	ns	**	ns				
		$\delta^{15}N$	ns	**	ns	**	**	**	ns		ns	**					
		St	*		**		**		**		**	**					
Mana		$\delta^{13}C$	**		**		**	**	ns	ns	*	ns	ns	**			
		$\delta^{15}N$	**	ns	**	ns	ns	ns	*		**	ns		**			
		St	**		**		**		**		**	**		**			
Tpra	S	$\delta^{13}C$	**		**		**	**	**	**	**	*	**	**	*		
		$\delta^{15}N$	**	ns	**	ns	ns	ns	**		**	ns		**	ns		
		St															
	L	$\delta^{13}C$	**		**		**	**	ns	ns	ns	ns	ns	**	ns	ns	
		$\delta^{15}N$	**	ns	**	*	ns	ns	ns		**	ns		**	ns	ns	
		St	*		**		**		**		**	ns		**	ns		

Note: An asterisk (*) indicates a significant difference (*, $\alpha = 5\%$; **, $\alpha = 1\%$) observed between two species for a given variable. When there was no significant difference between small (S) and large (L) individuals for either $\delta^{13}C$ or $\delta^{15}N$ in a species, results of interspecific comparisons are given for large individuals. Idem for stomach content comparisons. Amac, *Alticorpus macrocleithrum*; Amen, *Alticorpus mentale*; Cvir, *Copadichromis virginalis*; Dlim, *Diplotaxodon limnothrissa*; Dmac, *D. macrops*; Larg, *Lethrinops argenteus*; Lgos, *L. gossei*; Mana, *Mylochromis anaphyrmus*; Tpra, *Taeniolethrinops praeorbitalis*; ns, not significant; st, stomach content analysis.

different food webs with different basal $\delta^{15}N$ values (e.g., planktonic versus benthic), measurements of both planktonic and benthic algal $\delta^{15}N$ values indicate that the $\delta^{15}N$ of these two groups of autotrophs are generally within 1‰ of each other. Therefore, the observed range of 3.35‰ for fishes suggests that the species sampled represent a span of approximately one trophic level (3‰–5‰; Peterson and Fry 1987; Hesslein et al. 1991; Bootsma et al. 1996). Comparison of fish and potential food source isotopic composition may be complicated by temporal variations in food source isotopic enrichment. This has been observed in temperate lakes (e.g., Leggett et al. 1999, 2000), but few data are available for tropical systems. To determine the potential significance of temporal variation in Lake Malawi, we ex-

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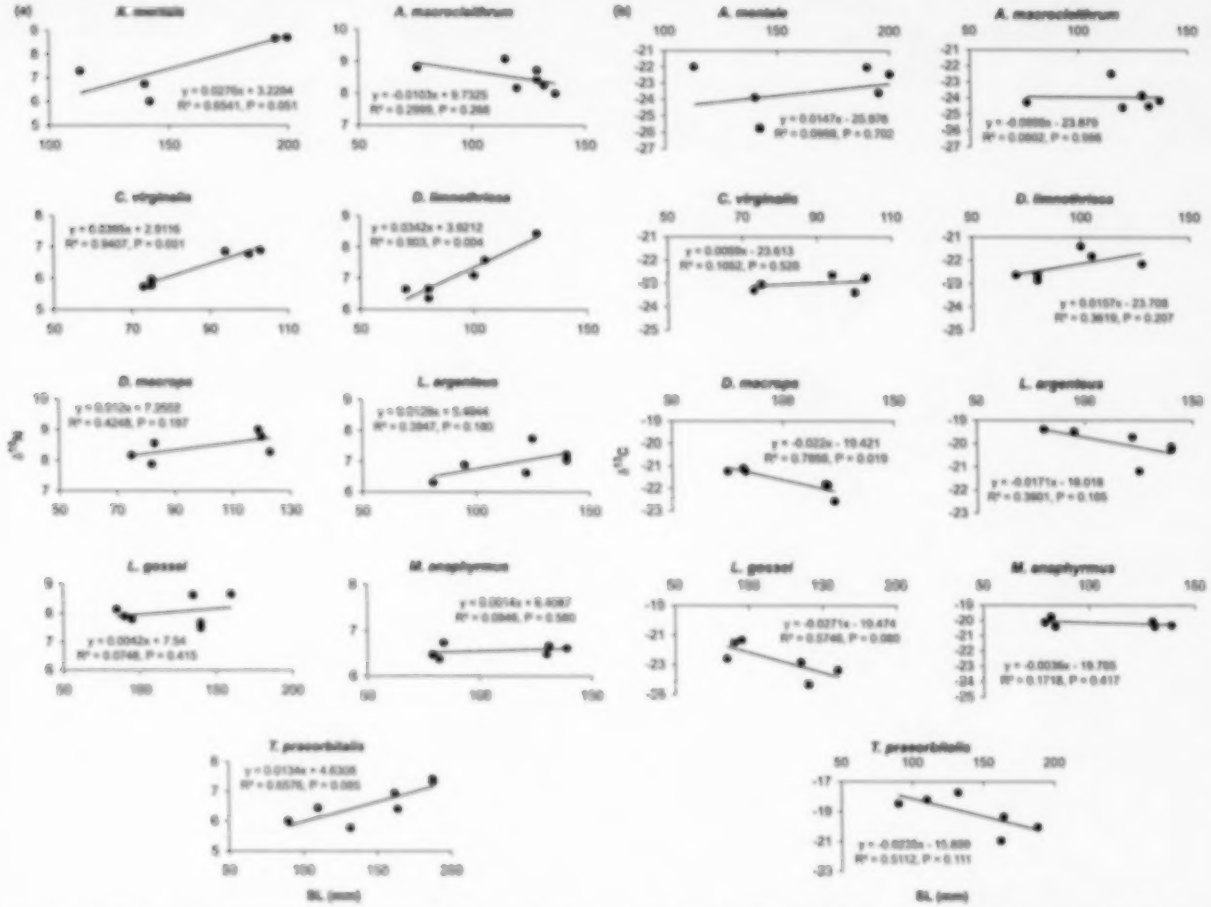
Fig. 2. Relationships between (*a*) standard length (SL) and $\delta^{15}N$ signatures and (*b*) SL and $\delta^{13}C$ signatures for each species in the SWA of Lake Malawi.



amined isotope data for samples that we previously collected in different seasons over several years. Samples included *Chaoborus edulis* adults, zooplankton collected from shallow and deep regions of the lake, the small clupeid *Engraulicyprus sardella*, and periphytic algae collected from rocks at a depth of 10 m in the southwest arm of the lake. The mean $\delta^{13}C$ of all pelagic samples combined was –23.9, with a standard deviation of 1.1 (n = 28), indicating that there is little temporal variability of pelagic $\delta^{13}C$ values, regardless of organism. This is not surprising for a tropical lake in which phytoplankton growth rates are high throughout the year (Bootsma 1993). Variability of periphytic algal $\delta^{13}C$ was slightly greater (mean = –11.7, standard deviation = 1.9, n = 6). Standard deviations of $\delta^{15}N$ for *E. sardella*, *C. edulis*, zooplankton, and benthic algae were 1.0, 1.0, 1.2, and 0.9, respectively. Although these samples do not include some of the potential food organisms sampled during the present study, they provide an indication of the potential magnitude of isotopic variability in pelagic and benthic lower trophic level organisms. These magnitudes are similar to or smaller than the statistically significant differences observed within and between fish species in this study, suggesting that these differences result more from different feeding habits than from temporal fluctuations in the isotopic composition of food organisms. For most of the nine fish species, stable isotope results were consistent with stomach content analysis.

Alticorpus macrocleithrum

Alticorpus macrocleithrum is a deep-water species found between 75 and 125 m (Duponchelle et al. 2003). As for most of the deep-water species, stomachs were often everted during trawl hauling. Only 22 specimens with remaining items in their stomachs were caught between November 1998 and May 1999. The average weight of the stomach contents was 31.2 mg, ranging from 6.4 to 96.8 mg for fishes of 103- to 137-mm standard length (SL, 31–67 g).

Alticorpus macrocleithrum had one of the highest mean $\delta^{15}N$ signatures (8.50, Fig. 3), just below that of the piscivorous large *A. mentale*. Large specimens in general exhibited slightly lighter $\delta^{15}N$ and enriched $\delta^{13}C$ signatures than small ones did (Figs. 2*a*, 2*b*). However, only a single small specimen was analysed for stable isotopic composition. As inferred from its anatomy by Stauffer and McKaye (1985), *A. macrocleithrum* appears to be a benthic invertebrate feeder (Fig. 1). Overall, 51% of the diet was not identifiable,

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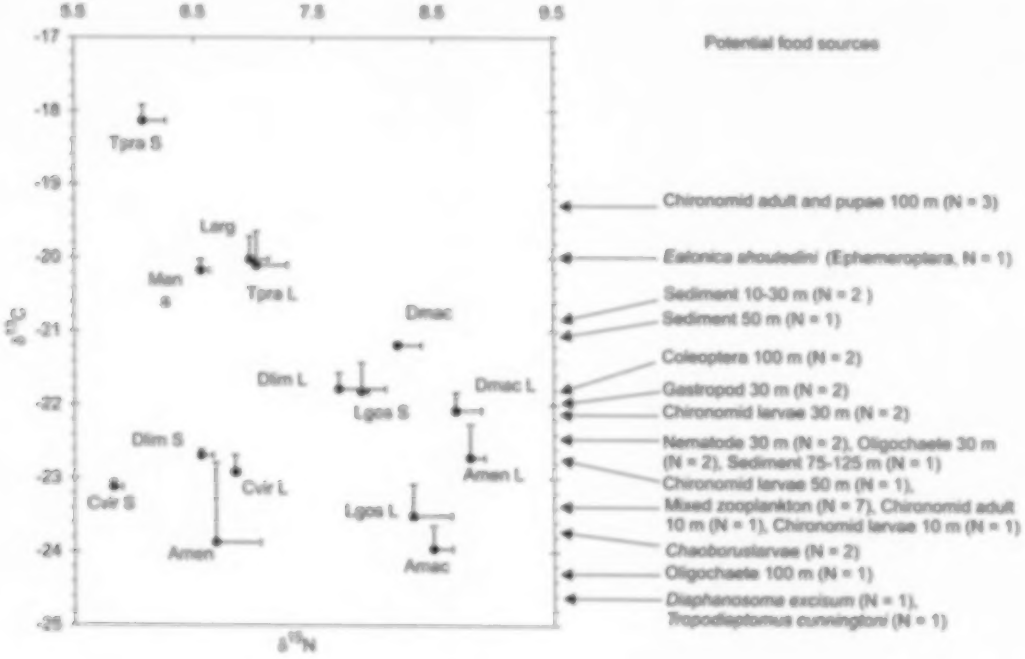
Fig. 3. Mean isotopic composition (±SEM) of some demersal cichlid fish species and their potential food sources in the SWA of Lake Malawi. Amac, *Alticorpus macrocleithrum*; Amen, *Alticorpus mentale*; Cvir, *Copadichromis virginalis*; Dlim, *Diplotaxodon limnothrissa*; Dmac, *D. macrops*; Larg, *Lethrinops argenteus*; Lgos, *L. gossei*; Mano, *Mylochromis anaphyrmus*; Tpra, *Taeniolethrinops praeorbitalis*. S and L refer to small and large specimens of a given species, respectively. The numbers correspond to the depth at which the samples were collected. Adult insects refer to the averaged $\delta^{13}C$ values of Hemiptera ($N = 1$), Ephemeroptera ($N = 1$), Corixidae ($N = 2$), and Coleoptera ($N = 2$). Mixed zooplankton refers to the averaged $\delta^{13}C$ values of various crustacean copepod species with similar signatures (*Diaptomus vruepelini*, $N = 1$; *Diaptomus dimixtus*, $N = 1$; *Mesocyclops neglectus*, $N = 2$; *Mesocyclops leukarti*, $N = 1$). Other zooplankton species with lighter signatures (*Diaphanosoma excisum* and *Tropodiaptomus cunningtoni*) were separated.



recorded either as detritus or "no ID". The other 49% was made up of chironomid larvae, *Chaoborus* larvae, insect larvae, diatoms, sand, and other items (fish scales, adult insects, cladocerans, copepods, gastropods, oligochetes, macrophytes, and other algae). The most important food items were chironomid larvae and lake fly (*Chaoborus*) larvae. Its isotopic composition was consistent with these observations since it was intermediate between the lightest $\delta^{13}C$ signatures (zooplankton: *D. excisum*, *Tropodiaptomus cunningtoni*, and Oligochaetes at 100 m) and the heavier *Chaoborus* larvae, average zooplankton and sediment between 75 and 125 m (Fig. 3). Although the $\delta^{13}C$ of chironomid larvae at 100 m was not measured, it might be inferred from the chironomid larvae $\delta^{13}C$ values at 30 m and 50 m that it would have been close to that of *A. macrocleithrum*. Owing to its short gut and deep-water existence, Stauffer and McKaye suggested that *A. macrocleithrum* does not feed on algae. However, at every sampled month except February (0.3%, Appendix A), diatoms constituted between 1.4% and 10.5% of the diet and averaged 4.8%. Diatoms might be ingested incidentally with sediment and sand while foraging to catch invertebrates. However, diatoms accounted for 10.5% of the diet in November, when only a small quantity of sand had been ingested, and for 4.1% in March, when almost no sand was ingested (Appendix A). Therefore, the proportion of diatoms ingested appeared too high to be incidental.

Alticorpus mentale

Alticorpus mentale is also a deep-water species mostly abundant between 75 and 125 m (Duponchelle et al. 2003). Because stomachs were almost always empty, all specimens from the entire catch were checked for intact stomachs. Only 14 specimens had remaining items in their stomachs during the period November 1998 – May 1999. The average weight of the stomach contents was 1374.8 mg, ranging from 10.2 to 6549.2 mg for fishes of 110- to 245-mm SL (25–279 g).

As expected from its morphology, *A. mentale* is a piscivore. Overall, 60% of its diet consisted of adult cichlid fishes (Fig. 1), often *Aulonocara minutus*. However, the small specimens (110–117 mm) had a diet that was significantly different (60% copepods, $p < 0.001$) from that of the large ones (170–245 mm), which fed mainly on other cichlid fishes (70%, Appendix A). Carbon isotopic composition of small *A. mentale* matched these observations (Fig. 3), being intermediate between the different zooplankton species (enriched mixed zooplankton species and depleted *D. excisum* and *T. cunningtoni*). Other items in the *A. mentale* diet were cichlid fry, scales, eggs, chironomid larvae, *Chaoborus* lar-

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vae, insect pupae, crustacean zooplankton, nematodes, sand, macrophytes, and other algae. The large specimens (190- to 200-mm SL) of *A. mentale* had the highest $\delta^{15}N$ signature, as expected from their almost strictly piscivorous habits (Fig. 3). Their position along the $\delta^{13}C$ range suggests that the fish species they consume rely on a phytoplankton-based (–22‰ to 23‰) food chain rather than on a benthic algal-based food chain (–8‰ to –16‰, Bootsma et al. 1996).

Copadichromis virginalis

Copadichromis virginalis mainly occurs at depths between 30 and 50 m in the north of the SWA (Duponchelle et al. 2003). Everted stomachs were not a problem, and 30 specimens were analysed between November 1998 and May 1999. The average weight of the stomachs contents was 68.7 mg, ranging from 18 to 190 mg for fishes of 70- to 115-mm SL (8–37 g).

Copadichromis virginalis is known as a member of the zooplanktivorous *utaka* group (Iles 1971; Fryer and Iles 1972; Turner 1996). Indeed, more than 95% of the diet was made of zooplankton, mainly copepods (Fig. 1). It was only in this species that a significant amount of cladocerans were found. Larger specimens had slightly more cladocerans in their diets than small specimens did (Appendix A). Other ingested items were fish scales, chironomid larvae, *Chaoborus* adults and larvae, insect adults and larvae, nematodes, macrophytes, other algae, and detritus. *Copadichromis virginalis* had amongst the lowest $\delta^{15}N$ in muscle. Stomach content analyses were supported by its isotopic composition, right in the range of the mixed zooplankton species (Fig. 3). The $\delta^{15}N$ difference observed between small and large specimens is likely due to a selective predation upon different zooplankton species. Large specimens of *C. virginalis* appear to feed more upon larger predatory zooplankton species than small ones do.

Diplotaxodon limnothrissa

Diplotaxodon limnothrissa was found at depths of 50–125 m, but was mostly abundant between 75 and 100 m (Duponchelle et al. 2003). Despite their deep-water existence, stomachs were not always everted after hauling, and 31 specimens were analysed. The average weight of the stomach contents was 66 mg, ranging from 8 to 272 mg for fishes of 101- to 145-mm SL (20–48 g).

Turner (1994) described *D. limnothrissa* as a zooplankton feeder, with specimens above 12 mm SL feeding mainly on copepods and small specimens of 3 mm feeding on chaoborid larvae and copepods. Allison et al. (1996*a*) reported a mixed diet composed of crustacean zooplankton, *Chaoborus* larvae, *E. sardella* (Usipa) larvae and juveniles, and occasionally phytoplankton. Our observations also suggested a mixed diet: 71% of the diet was made of copepods, *Chaoborus* larvae, adult insects, and Usipa larvae (Fig. 1). This is supported by its $\delta^{13}C$ signature (Fig. 3), which is slightly above those of zooplankton species, *Chaoborus* larvae, and mixed adult insects, and below the signature of some insect species such as *Eatonica shoutedini* (Ephemeroptera). Adults insects such as Coleoptera are not likely to account for an important part of *D. limnothrissa* diet because their mean $\delta^{15}N$ signature is only about 1‰ lighter (6.58 ± 0.28). The isotopic composition of adults was consistent with a diet partly made of small *E. sardella* (<5 mm), which have a $\delta^{15}N$ signature about a trophic level (3‰) lighter (average 4.8‰; Bootsma et al. 1996). The $\delta^{13}C$ signature of small *D. limnothrissa* was consistent with a diet based on *Chaoborus* larvae and copepods, as reported by Turner (1996). Large *D. limnothrissa* specimens (100–128 mm SL) had a higher average $\delta^{15}N$ signature (7.71 ± 0.68) than the small specimens (70–80 mm: 6.56 ± 0.17), indicating that they relied on food sources of a slightly higher trophic level (Fig. 3). The remaining part of *D. limnothrissa* diet was composed of unidentified material, detritus and other items (cichlid fry, scales, fish eggs, chironomid larvae, cladocerans, bivalves, sand, diatoms, and other algae). Unlike that of *A. mentale* and *C. virginalis*, the diet composition of *D. limnothrissa* varied strongly among months, being dominated by copepods in November 1998, April and May 1999, by *E. sardella* larvae in January 1999, or by *Chaoborus* larvae in March 1999 (Appendix A).

Diplotaxodon macrops

Diplotaxodon macrops is a deep-water species found at depths of 75–125 m (Duponchelle et al. 2003). Stomachs with measurable contents were not as frequent as those found for *D. limnothrissa*, and only 20 specimens were analysed between November 1998 and May 1999. The average weight of the stomach contents was 61.2 mg, ranging from 5.4 to 157.4 mg for fishes of 85- to 118-mm SL (17–42 g).

Turner (1996) reported *D. macrops* was zooplanktivorous. Our results tend to support this statement, as 55% of the overall diet comprised copepods and *Chaoborus* larvae (Fig. 1). Its mean $\delta^{13}C$ isotopic signature supported these results (Fig. 3). The remaining part of the diet was composed of chironomid larvae, sand, detritus, unidentified material, and other items (scales, adult insects, cladocerans, macrophytes, diatoms, and other algae). It is important to note that in months when more than only one or two specimens were examined, zooplankton accounted for 84%–99% of the diet (December 1998, April and May 1999) (Appendix A). Chironomid larvae constituted a significant part of the diet only once in November 1998, with a single fish examined. *Chaoborus* larvae were dominant items in February and May 1999 (Appendix A). The diet composition of *D. macrops* was generally similar to that of *D. limnothrissa*, with copepods and *Chaoborus* larvae accounting for most of their diets. However, their feeding strategies appeared to be slightly different, as benthic invertebrates and significant amounts of sand were regularly found in *D. macrops* stomachs, suggesting a benthic foraging activity not observed in *D. limnothrissa*. *D. macrops* $\delta^{15}N$ and $\delta^{13}C$ signatures also distinguish it from *D. limnothrissa*. Adults relied on enriched N sources and slightly depleted C sources, whereas small individuals relied on enriched N and C sources compared with *D. limnothrissa* (Fig. 3). The few small specimens (<90-mm SL) for which stomachs were found with remaining items, contained almost exclusively copepods and *Chaoborus* larvae (Appendix A). However, as the mean $\delta^{13}C$ signature of small *D. macrops* was about 2‰ greater than the mean zooplankton signature, they must also rely on more enriched carbon sources. The significant amounts of sand and benthic invertebrates encountered in stomach contents suggest a benthic foraging activity. The consumed benthic

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invertebrates probably rely to a significant degree on periphyton, which has an enriched $\delta^{13}C$ signal (–8‰ to –16‰; Bootsma et al. 1996). Also, the fact that small *D. macrops* belong to a higher trophic level (mean $\delta^{15}N$ 8.20‰) than the exclusively zooplanktivorous small *C. virginalis* (5.83‰) indicates they mostly rely on food sources other than zooplankton. In a previous study, *Chaoborus* larvae were found to have a $\delta^{15}N$ of between 5.5 and 7.5 (H. Bootsma, unpublished data), indicating that this organism may account for an important part of the diet of *D. macrops*.

Lethrinops argenteus and *Taeniolethrinops praeorbitalis*

Lethrinops argenteus (= *L. longipinnis* orange head) mainly occurs at depths between 10 and 30 m (Duponchelle et al. 2003). The stomachs of 34 specimens were examined during the period November 1998 – May 1999. The average weight of the stomachs contents was 54.2 mg, with a range of 6–197 mg for fishes of 92- to 142-mm SL (37–87 g). Diet composition of *L. argenteus* was essentially made up of chironomid larvae (Fig. 1), but also included sand, detritus, unidentified material, and other items (scales, fish eggs, insects adults, larvae and pupae, crustacean zooplankton, nematodes, gastropods, bivalves, macrophytes, diatoms, and other algae). Given the nature of the main ingested food item and the presence of large amounts of sand in each sample, this species seems to be a benthic invertebrate feeder, as suggested by its morphology.

Taeniolethrinops praeorbitalis is a shallow water species encountered at depths of 10–30 m (Duponchelle et al. 2003). The stomachs of 13 specimens were examined between November 1998 and May 1999. The average weight of the stomach contents was 49.3 mg, with a range of 5–142 mg for fishes of 97- to 193-mm SL (24–166 g). This species is known to feed primarily on chironomid larvae (Fryer 1959; Eccles and Trewavas 1989; Turner 1996). However, specimens examined by Fryer (1959) were sometimes full of nematodes. Jackson (cited by Turner 1996) reported that *T. praeorbitalis* fed mostly on *Chaoborus* larvae. Konings (1995) reported its main food is insect larvae. Detritus, diatoms, and sand were also reported to occur in its diet (Turner 1996). The 13 specimens we examined fed largely on chironomid larvae, which averaged 46% of the diet (Fig. 1). Overall, copepods accounted for 13% of stomach content, though they were present only in small specimens (Appendix A). The remaining components of the diet were large amounts of sand, detritus, unidentified materials, and other items (scales, insect adults and pupae, nematodes, macrophytes, cladocerans, diatoms, and other algae). No temporal variability in diet composition was noticed, the only variation being the relative proportions of chironomids and sand between months (Appendix A). The small specimens (90- to 130-mm SL) analysed tended to have a smaller proportion of chironomid larvae in their stomachs and larger proportions of copepods and plant material than did large individuals (165–195 mm) (Appendix A).

Lethrinops argenteus and *T. praeorbitalis* had very similar feeding strategies and did not differ in diet composition or in adults' isotopic composition (Table 1). Only the young of *T. praeorbitalis* had enriched $\delta^{13}C$ signatures (Fig. 3; Table 1). Stomach content analysis for both species showed diet composition mainly consisted of chironomid larvae, sand, detritus, and other items. However, *L. argenteus* and *T. praeorbitalis* $\delta^{13}C$ signatures were more enriched than expected if they were relying only on chironomid larvae at depths of 10 and 30 m. As these species are bottom feeders ingesting large amounts of sand, they probably also have other food sources with enriched carbon signals, such as periphyton (Bootsma et al. 1996) or other plant material, which were indeed regularly found in stomachs (macrophytes and unidentifiable algae). Stomach analysis revealed that apart from chironomid larvae, zooplankton and plant material were important components of the diet for both species. However, as the zooplankton has a more depleted $\delta^{13}C$ signal than that of chironomid larvae found in shallow water, it cannot account for the enriched $\delta^{13}C$ signature of small *T. praeorbitalis* and *L. argenteus* individuals compared with large ones (Fig. 3). Oligochaetes, which are difficult to identify in stomachs when digested, have been found to account for more than 50% of the *T. praeorbitalis* diet (W. Darwall, IUCN/SSC UK Office, 219c Huntingdon Road, Cambridge CB3 ODL, UK; will.darwall@ssc-uk.org, personal communication) and might have constituted an important part of the unidentified material in our analysis. Unfortunately, we did not sample a sufficient number of oligochaetes at 10 m for stable isotope analysis, where all the *T. praeorbitalis* analysed for isotopic composition were caught. Nevertheless, given the large difference in $\delta^{13}C$ signatures between oligochaetes at 100 and 30 m (Fig. 3), oligochaetes are likely to have an enriched $\delta^{13}C$ signature in the shallow waters. The benthic foraging habits of *T. praeorbitalis* and *L. argenteus* suggest that they may rely on periphyton with enriched $\delta^{13}C$ signatures found in sediment (Bootsma et al. 1996). The higher $\delta^{13}C$ and lower $\delta^{15}N$ suggest that small *T. praeorbitalis* and *L. argenteus* may rely even more than adults do on benthic algae, and may occupy a shallower habitat.

Lethrinops gossei

Lethrinops gossei is a deep-water species mainly caught at depths of 75–125 m (Duponchelle et al. 2003). Despite its deep-water existence, non-everted stomachs were found, though they were seldom full. The stomachs of 21 specimens were examined between November 1998 and May 1999. The average weight of the stomach contents was 72.7 mg, ranging from 5 to 210 mg for fishes of 101- to 155-mm SL (33–118 g).

Turner (1996) reported that this species fed on benthic arthropods, and Allison et al. (1996*b*) found *Chaoborus* larvae and pupae to make up to 94% of its diet, with some chironomid larvae. In contrast, our results indicated a mixed diet of benthic invertebrates and zooplankton (Fig. 1). Over the sampling period, dominant food items were *Chaoborus* larvae, chironomid larvae, diatoms, and copepods, together making up to 76% of the *L.gossei* diet. Its $\delta^{13}C$ signature, in the range of that of *Chaoborus* larvae and zooplankton, might indicate that this species relies primarily on these food sources (Fig. 3). However, as we do not have stable carbon isotope data for chironomid larvae in deep waters, nor of diatoms specifically, their potential importance in the *L. gossei* diet cannot be excluded. The remaining part of the diet was made of unidentified material, detritus, and other items (scales, insects adults, larvae and pupae, nematodes, macrophytes, and other algae). Diet composition was highly variable from one month to another, being dominated by diatoms in December 1998 and January 1999, by chirono-

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mid larvae in April 1999, and by *Chaoborus* larvae in March and May 1999 (Appendix A). As only a very small amount of sand was found in the stomachs, the large amounts of diatoms ingested suggest some planktonic feeding. *Lethrinops gossei* had among the highest average $\delta^{15}N$ signatures (8.12) of fishes sampled as part of this study (Fig. 3). Small specimens had enriched $\delta^{13}C$ and slightly depleted $\delta^{15}N$ values compared with those of large specimens. The smallest specimen found with remaining items in its stomachs was 101-mm SL, and diatoms made up 44% of its diet. Small *L. gossei* may rely even more upon diatoms than the adults, which could account for the difference in isotopic composition.

Mylochromis anaphyrmus

Mylochromis anaphyrmus frequents the shallow waters between 10 and 50 m (Duponchelle et al. 2003). The stomachs of 36 specimens were examined between November 1998 and May 1999. The average weight of the stomachs contents was 45.6 mg, ranging from 8 to 290 mg for fishes of 84- to 151-mm SL (16–125 g).

This species is known as a gastropod feeder (McKaye et al. 1986; Konings 1995; Turner 1996), although copepods, chironomids, algal remains, and arthropod material are sometimes found (Turner 1996). Most of the specimens we examined had large quantities of snail remains in their guts. However, what is presented here is only the stomach content analysis. Gastropods averaged 15% (4%–44%) of the stomach contents (Fig. 1). Chironomid larvae accounted for 41%, adult insects for 10%, and crustacean zooplankton for 5%. However, the isotopic composition of *M. anaphyrmus* was consistent with a diet based mostly on gastropods, for which the average signatures at 30 m (the most common depth of the species in the sampled area) were –22.02 and 3.13 for $\delta^{13}C$ and $\delta^{15}N$, respectively (Fig. 3). Often a food source is 0.5‰–1‰ enriched in ^{13}C relative to its consumer (Peterson and Fry 1987). The 1.85‰ found here might be explained by a preference for particular gastropod species with slightly lighter signatures or by feeding partly at shallower depths, where gastropods can be expected to have enriched signals (Bootsma et al. 1996). The remaining part of stomach content was made of sand, unidentified material, and other items (scales, chironomid pupae, *Chaoborus* larvae, insect pupae and larvae, nematodes, bivalves, macrophytes, diatoms, and other algae). Individuals below 100 mm SL tended to have higher proportions of chironomid larvae in their stomachs: more than 99% for the two smallest specimens (80 and 84 mm) (Appendix A).

With the exception of a few species that actually feed upon fish (e.g., *A. mentale*, *D. limnothrissa*), the presence of fish scales in almost every stomach analysed, regardless of species, is probably an artifact caused by the crowding of fishes during the trawl hauling. Indeed, at every haul, medium and large fish, including nonpiscivorous species, had small fish stuck in their mouths.

Resource partitioning

Despite the high variability of stomach fullness encountered during this study, particularly for the deep-water species, a good correspondence between the results of stomach content and stable isotope analyses was observed for most of the nine fish species. Nevertheless, the use of both stomach content and stable isotope analyses ($\delta^{13}C$ and $\delta^{15}N$) proved very useful in elucidating dietary differences between species. Every species differed significantly from the others by at least one of the three types of analyses (stomach content, $\delta^{13}C$ and $\delta^{15}N$), demonstrating the complementarity of these approaches (Table 1).

Species with very different feeding habits (reflected in their stomach content), such as *C. virginalis*, small *D. limnothrissa*, large *L. gossei*, and large *A. mentale* (Fig. 3), would have been impossible to distinguish without a combined analysis of $\delta^{13}C$ and $\delta^{15}N$ signatures. They only covered a $\delta^{13}C$ range of 0.4‰, but were discriminated by a 2.97‰ $\delta^{15}N$ range. Species with a narrower feeding regime, such as *A. mentale* or *C. virginalis*, had an isotopic composition closely matching the stomach content observations. For *M. anaphyrmus*, despite the observed dominance of other food items in the stomachs, the isotopic composition confirmed the previously reported snail diet of the species (McKaye et al. 1986; Eccles and Trewavas 1989; Konings 1995). The stomach contents we observed reflect feeding habits for several hours prior to capture, which appear to have been different from the longer term feeding habits, as reflected in isotopic composition. Stomach content analysis indicated temporal trends of diet composition for both *L. argenteus* and *T. praeorbitalis*, mainly dominated by chironomid larvae. However, stable isotope analysis suggested that algal food items were likely playing an important role in the diet of these species, particularly for the small specimens. Differences in feeding habits and in isotopic composition are expected between species as morphologically different as *A. mentale* and *C. virginalis* or *T. praeorbitalis*. However, significant isotopic differences were found (Table 1) between closely related species with very similar stomach contents, such as *D. limnothrissa* and *D. macrops*, and between typical invertebrate feeders with similar stomach content compositions and identical depth preferences, such as *L. argenteus* and *T. praeorbitalis*. Species with a complex feeding regime, such as *A. macrocleithrum*, *D. limnothrissa*, *D. macrops*, and *L. gossei*, showed important temporal variations in diet composition (Appendix A). These four species heavily fed upon *Chaoborus* larvae when available. For each of these species, *Chaoborus* larvae were dominant items in their stomachs in exactly the same months, March and May, and only in these months (Appendix A). This suggests that the observed feeding regimes were related to temporal fluctuations in food resources, although we do not have data to back up this hypothesis. These observations would not have been possible without monitoring stomach contents, and they highlight the complementary nature of stomach content and stable isotope approaches in the study of feeding habits and trophic patterns of complex fish communities.

These observations also emphasised the importance of *Chaoborus* for the deepwater demersal fishes. *Alticorpus macrocleithrum*, *D. limnothrissa*, *D. macrops*, and *L. gossei* averaged 30–43% of the total biomass in the deep waters (75–125 m) over a 1-year monthly demersal trawl survey in the SWA of the lake (Duponchelle et al. 2003). Added to other species relying heavily on *Chaoborus*, such as the catfish *Synodontis njassae* (Allison et al. 1996*a*, 1996*b*), which averages about 10% of the total fish biomass in the deep wa-

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ters (Duponchelle et al. 2003), about 50% of the fish biomass depends, at least partly, upon *Chaoborus*. This supports the recent work of Allison et al. (1996*a*, 1996*b*), and suggests that fish production would not be increased by the introduction of other planktivorous fish species, as has been suggested in the past (Turner 1982; Walczak 1982). Our results also partially support the hypothesis of Allison et al. (1996*b*) that "because *C. edulis* feeds on crustacean zooplankton, demersal fish production may therefore be principally sustained through the pelagic food chain rather than from benthic detrital sources." They only partially support this hypothesis because they do confirm the importance of *C. edulis* as a food source for benthic fishes, but they also show that there is a heavy reliance upon benthic prey organisms for most species. Isotopic composition clearly illustrates the diet separation among these demersal fish: one on the hand there is the pelagic phytoplankton food chain, centred near a $\delta^{13}C$ of –23‰ with at least three trophic levels (zooplankton and *Chaoborus* larvae, zooplanktivorous fishes, such as *E. sardella* and *C. virginalis*, and fishes of a higher trophic level such as *A. mentale*, *A. macrocleithrum*, *D. limnothrissa*, *D. macrops*, and *L. gossei*, some of which feed upon other fishes). On the other hand, there is an ascending line towards heavier carbon and lighter nitrogen sources represented by *L. argenteus* and *T. praeorbitalis*, which most likely represents, in large part, a periphyton-based food web. In fact, given the much heavier $\delta^{13}C$ signature of periphyton (Bootsma et al. 1996), the shift to heavier carbon and lighter nitrogen likely represents mixed feeding on both the periphyton-based source and the phytoplankton-based source. This is interesting, in that it suggests that benthic algal production is contributing to energy flow of the offshore fishes at depths of 10–30 m.

These examples demonstrate the existence of distinct feeding strategies between species with apparently similar diets and feeding behaviors, and support the assertion that important resource partitioning exists among Lake Malawi haplochromine cichlids (Bootsma et al. 1996; Genner et al. 1999*a*; Turner 1996). As suggested by Bootsma et al. (1996), this partitioning can be achieved by either of the following: (1) feeding on different food types, such as *A. macrocleithrum*, *A. mentale*, *Diplotaxodon macrops*, and *L. gossei* (each of these species inhabit the deep waters below 75 m, but feed on different sources), or (2) feeding on similar food types but from different locations (i.e., spatial partitioning), such as *D. limnothrissa* and *D. macrops*. Although they had similar stomach contents (Table 1), their feeding strategies were different: the presence of benthic invertebrates and sand in *D. macrops* suggested a benthic foraging activity not observed in *D. limnothrissa*, which was supported by their different $\delta^{15}N$ signatures.

If the apparent partitioning of resources is critical for the maintenance of these species-rich fish communities, then changes in water quality and habitat structure may have serious implications for diversity in Lake Malawi and other African rift valley lakes. Studies in Lake Tanganyika (Alin et al. 1999; Donohue and Irvine 2004) provide strong evidence that increased sediment loads result in reduced diversity of benthic invertebrates. Recent data (Bootsma et al. 2003; Hecky et al. 2003) suggest that riverine inputs of nutrients and suspended sediment to Lake Malawi are increasing, and nutrient and sediment loads from some rivers draining heavily impacted watersheds are exceptionally high. The data presented here suggest that food resource partitioning is a common practice within the species-rich demersal fish community of Lake Malawi; therefore, any decline in diversity of benthic invertebrates resulting from these increased sediment loads will likely increase the potential for competitive exclusion within the fish community.

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(Appendix A follows.)

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Appendix A

Fig. A1. Overall and monthly diet composition (% stomach content) of nine demersal cichlid fishes in the SWA of Lake Malawi. "Others" refers to materials such as scales, fish eggs, insects adults, larvae, and pupae, crustacean zooplankton, nematodes, gastropods, bivalves, macrophytes, diatoms, and other algae making up less than 2% of the diet. Unidentifiable materials were recorded as "No ID". Different letters indicate significant differences between months ($\alpha = 0.05$). The overall diet composition was divided between small (S) and large (L) specimens when small individuals were analyzed. A distinction was made between small and large individuals when a significant correlation was observed between size and either $\delta^{15}N$ or $\delta^{13}C$ in Fig. 2. For *Alticorpus mentale*, small ranged from 110 to 117 mm and differed significantly from large specimens (170–245 mm, $p < 0.001$). For *Copadichromis virginalis*, small ranged from 70 to 85 mm and did not differ from large specimens (90–115 mm, $p = 0.525$). For *Diplotaxodon macrops*, small ranged from 85 to 99 mm and did not differ from large specimens (105–118 mm, $p = 0.679$). For *Mylochromis anaphyrmus*, small ranged from 80 to 99 mm and did not differ from large specimens (101–151 mm, $p = 0.152$). For *Taeniolethrinops praeorbitalis*, small ranged from 97 to 127 mm and did not differ from large specimens (168–183 mm, $p = 0.864$). (Figure A1 is concluded on the following pages.)

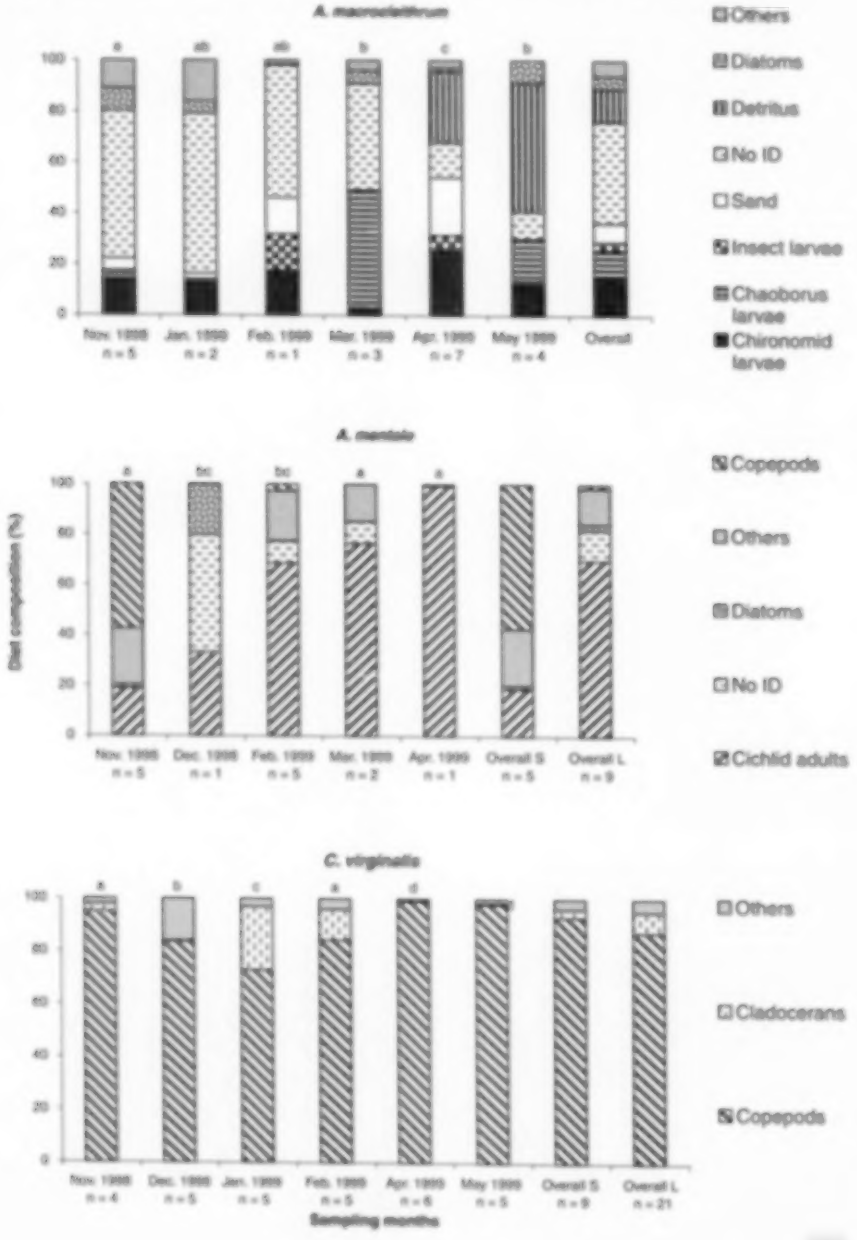

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Fig. A1 (*continued*).

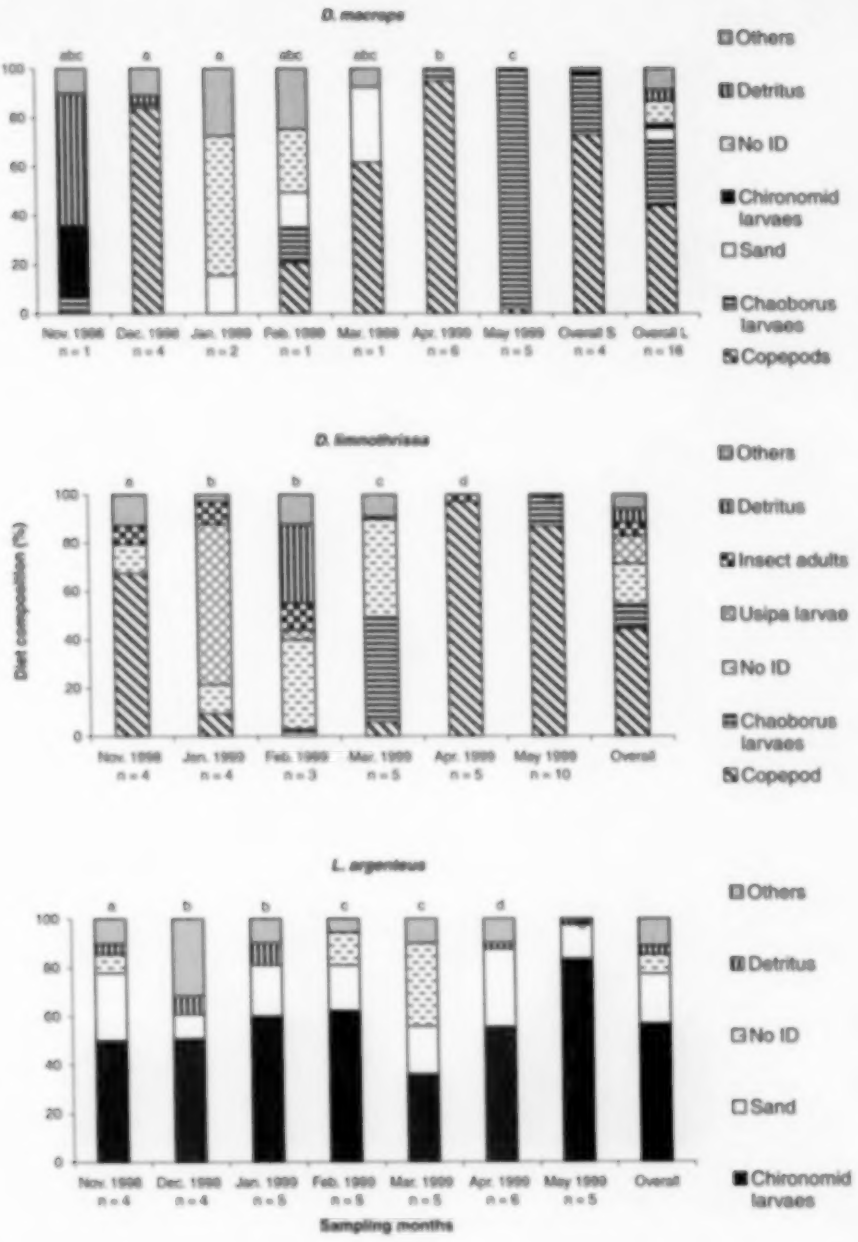

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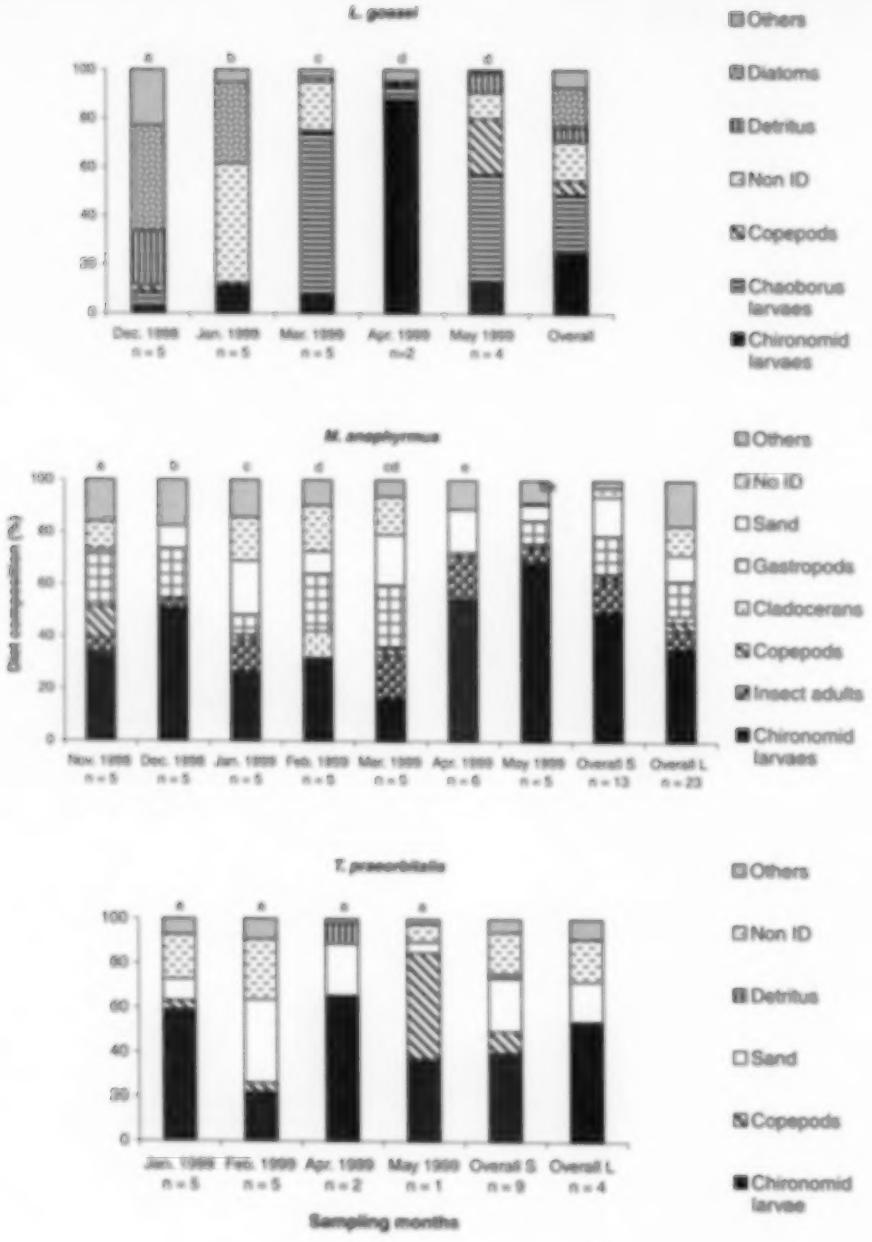
Fig. A1 *(concluded).*



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A statistical model for in-season forecasts of sockeye salmon (*Oncorhynchus nerka*) returns to the Bristol Bay districts of Alaska

Saang-Yoon Hyun, Ray Hilborn, James J. Anderson, and Billy Ernst

Abstract: We developed a model for in-season age-specific forecasts of salmon returns using preseason return forecasts, age composition of in-season returns, cumulative in-season returns by fishing district, and age composition and an index of abundance from an in-season test fishery. We apply this method to the sockeye salmon (*Oncorhynchus nerka*) fishery in the Bristol Bay districts of Alaska. The model generates point estimates and Bayesian probability distributions for return numbers by age and river, and it provides an integrated framework for including all of the major data sources currently used in in-season forecasting. We evaluated model performance using early-season data from 1999–2001 and compared the effects of four information sets on forecast accuracy. The four information sets were as follows: I, district-specific inshore return data; II, inshore return data and test fishery data; III, inshore return data and preseason forecasts; IV, inshore return data, test fishery data, and preseason forecasts. Forecasts from information sets II, III, and IV were less biased than those from information set I. However, in terms of the forecast interval, forecasts from information set II were best because the 95% highest posterior density regions of forecasts from information set II covered the actual returns most frequently.

Résumé : Nous avons élaboré un modèle spécifique à l'âge qui prédit les retours des saumons pendant la saison même à l'aide des prédictions des retours faites avant la saison, de la composition en âges des retours pendant la saison, des retours cumulatifs pendant la saison selon les districts de pêche, ainsi que de la composition en âge et d'un indice d'abondance provenant d'une pêche expérimentale durant la saison. Nous appliquons la méthode à la pêche de saumons rouges (*Oncorhynchus nerka*) des districts de la baie de Bristol en Alaska. Le modèle fournit des estimations ponctuelles et des distributions de probabilité bayésienne des nombres de retours en fonction de l'âge et de la rivière et il procure un cadre intégré pour l'inclusion de toutes les sources principales de données couramment utilisées pour faire des prédictions au cours de la saison. Nous avons évalué la performance du modèle en utilisant des données récoltées tôt dans la saison en 1999–2001 et comparé les effets de quatre séries de données sur la justesse de la prédiction. Les quatre séries de données étaient : I, les données de retour au bord en fonction des districts; II, les données de retour au bord et les données de la pêche expérimentale; III, les données de retour au bord et les prédictions faites avant la saison; et IV, les données de retour au bord, les données de la pêche expérimentale et les prédictions d'avant la saison. Les prédictions obtenues des séries de données II, III et IV ont moins de distorsion que celles provenant de la série I. Cependant, en ce qui a trait à l'intervalle de prédiction, les prédictions obtenues de la série de données II sont les meilleures, parce que 95 % des régions de densité a posteriori la plus élevée (HPD) des prédictions obtenues à partir de la série II correspondent le plus souvent aux retours réels.

[Traduit par la Rédaction]

Introduction

A trend in fisheries modeling and analysis has been to develop statistical methods that use all sources of available data to estimate population abundance or other population parameters (Hilborn 2003). In age-structured stock assessments, modern approaches generally use indices of abundance, age distribution, length distribution, and often tagging data in an integrated statistical framework (Quinn and Deriso 1999). This approach can be extended beyond age-structured stock assessment models to other fisheries applications that have multiple data sources.

Managing the Bristol Bay, Alaska, sockeye salmon (*Oncorhynchus nerka*) (Fig. 1), like other anadromous fisheries, involves maximizing harvest while meeting spawner escapement goals and conserving the genetic characteristics

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S. Hyun.[1,2] Quantitative Ecology and Resource Management, University of Washington, Box 352182, Seattle, WA 98195, USA.
R. Hilborn, J.J. Anderson, and B. Ernst.[3] School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, WA 98195, USA.

[1]Corresponding author (e-mail: syhyun@alumni.washington.edu).
[2]Present address: Columbia River Inter-Tribal Fish Commission, 729 NE Oregon Street, Suite 200, Portland, OR 97232, USA.
[3]Present address: Departmento de Oceanografía, Universidad de Concepción, Concepción, Chile.

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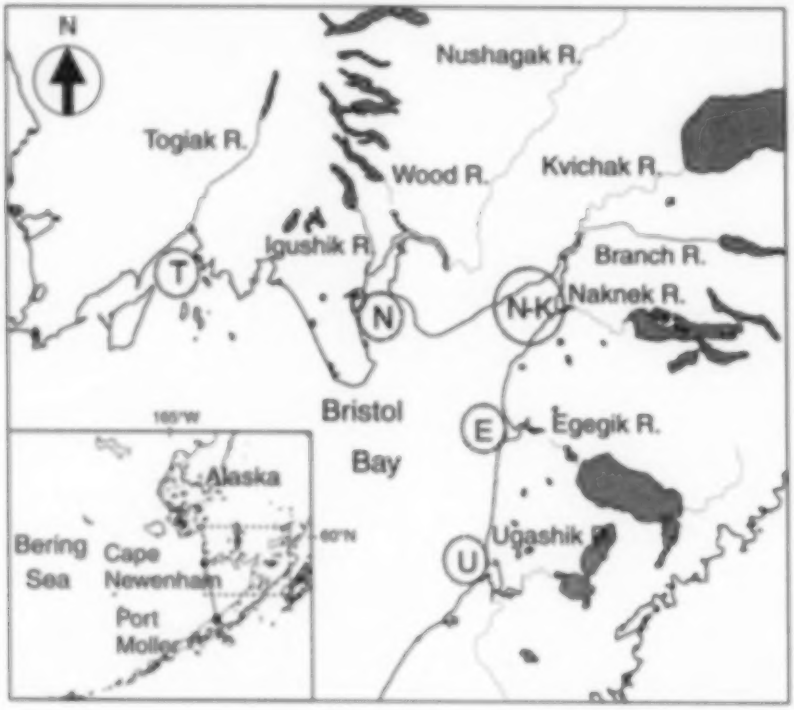
Fig. 1. Five estuaries and nine river systems in Bristol Bay, Alaska, USA. The solid line in the box indicates a transect line between Port Moller and Cape Newenham. Estuary abbreviations are as follows: T, Togiak; N, Nushagak; N–K, Naknek–Kvichak; E, Egegik; U, Ugashik.



of the stocks comprising the run. To achieve these goals, managers need to distribute harvest over the return season and across the stocks, which requires accurate estimates of the size and timing of each stock within a commercial fishery prior to the completion of the run. In-season run size estimates are also of use to commercial fishermen who make daily decisions about where to fish and processors who need to allocate their fleet of tenders to different areas to service their fishing fleets.

In-season forecasting of run timing and the contributions of each individual stock (identified by its fishing district) is not a trivial task because of the large year-to-year variability in total run size, which has varied between 2.2 and 60.5 million fish in the Bristol Bay fishery. Management is also complicated by the very short duration of the return, which mostly occurs over a 2-week period (Burgner 1980), and by the variable timing and returns of fish to each of the five districts year-to-year.

Currently, preseason forecasts are made 6 months before the June–July return season by the Alaska Department of Fish and Game and the University of Washington Alaska Salmon Program (UW ASP). During the fishing season, managers compare total returns-to-date with historical returns-to-date, the age composition of the returns, and data from the in-season Port Moller test fishery (Fig. 1) to subjectively estimate whether the run is early or late and large or small. Based on this information, forecasts are updated daily during the run season and managers regulate fishing time daily in each district. However, there are no quantitative methods in place to use these data sources; the managers subjectively weigh the data and make their decisions based on the data and their experience and intuition.

The Port Moller test fishery, conducted from 10 June to 9 July, assesses the daily abundance of returning sockeye salmon a week prior to the fish arriving in the commercial fishing districts. Abundance is assessed using the catch per unit effort (CPUE) from standardized research drift gillnet stations between Port Moller and Cape Newenham (Fig. 1). A daily run size index (Rogers' index) is derived by weighting the stations according to the historical correlation of the CPUE with total return size. Until recently, in-season run size is estimated by a linear regression of the cumulative Rogers' index through a specified day of the test fishery (Mundy 1979; Rogers 1994; Rogers and Steen 2000). Other forecast methods have also been developed. Fried and Hilborn (1988) applied Bayesian theory to forecast the total return size by combining the preseason forecast, the Port Moller test index, and the total return-to-date. However, both the current forecast method and the Bayesian method forecast only the total run size. The Fried and Hilborn (1988) method did not use the age composition of the data from Port Moller and inshore return, but this information has become increasingly important to the managers, and in recent years, the primary motivation for operating the Port Moller test fishery has been to obtain age composition data. The existing quantitative methods are inadequate for determining harvest levels to meet the stock-specific escapement goals and for preserving stock genetics as revealed by the stock-specific run timing.

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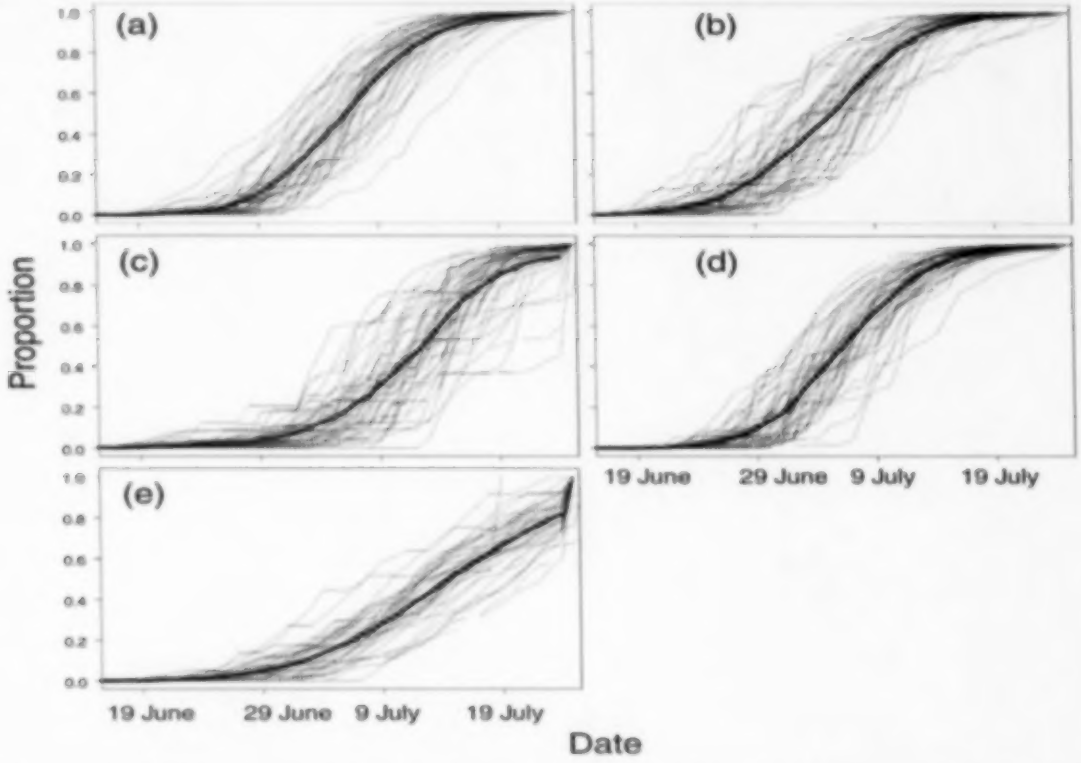
Fig. 2. Historical return proportions of sockeye salmon (*Oncorhynchus nerka*) to Bristol Bay, Alaska, by stock per day. Each line represents historical return proportion by day for 1955–2001, except for the Togiak stock, which started in 1958. The thick line is the mean of the cumulative run proportions per day. (*a*) Naknek–Kvichak stock; (*b*) Egegik stock; (*c*) Ugashik stock; (*d*) Nushagak stock; (*e*) Togiak stock.



In this paper, we develop a systematic in-season forecast that uses all available fishery and relevant biological data to predict age-specific returns to each of the five Bristol Bay districts and uses a Bayesian analysis to calculate the uncertainty in the predictions. We evaluate the forecast abilities of the model by hindcasting runs from 1999–2001 using only data prior to the in-season forecast day.

We focus on the accuracy (bias and precision) of early-season (24 June, 29 June, 4 July, and 9 July) stock-specific return forecasts because these are of primary interest to managers. Early-season forecasting is challenging because of a lack of early in-season data and large variability in run timing (Fig. 2). In terms of the cumulative run proportions for each specified day from 1955–2001, the mean values for the Naknek–Kvichak, Egegik, and Nushagak stock runs were ~1%–6% on 24 June, ~10%–18% on 29 June, and ~32%–43% on 4 July, respectively. The Ugashik and Togiak stock runs were ~0–2%, ~6–8%, and ~12–14%, respectively, on the same dates (Fig. 2). Finally, the algorithm can be implemented into software for use by fishery managers.

Methods

Data sources

The data sources collected in-season include (*i*) age composition obtained from scale samples of catch and escapement, (*ii*) daily catch and escapement by fishing district and escapement counting site, and (*iii*) standardized CPUE from the Port Moller test fishery and Rogers' index derived from the standardized CPUE (Table 1; Fig. 3). The historical data sets used were total return sizes, 1958–2001, Rogers' indices, 1985–2001, age-specific return sizes, 1985–2001, age-specific catches from the Port Moller test fishery, 1985–2001, and district-specific return proportions by day, available since 1955, except for the Togiak stock, which started in 1958 (Table 1; Fig. 3).

Statistical model

The overall approach was to treat the number of individuals returning to the four dominant age groups (1.2, 2.2, 1.3, and 2.3, which account for about 98% of all homing fish) for the five fishing districts as the 20 parameters of primary interest (see Appendix A, Table A1, for the expression of salmon age). Prior information for each of these parameters was obtained from preseason forecasts that are published annually. For each day of the fishing season, the data available up to that day are used to update the prior information using Bayes' law. For each data source, there is a likelihood that is described below.

For several of the data sources, there is a two-stage procedure. The likelihood of the data collected in-season, given the possible stock-specific returns by age, depends on pa-

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Table 1. Summary of the likelihood functions used to model in-season age-specific forecasts of sockeye salmon (*Oncorhynchus nerka*) returns to the Bristol Bay districts of Alaska.

In-season data	Historical data or parameters from data	Likelihood	Parameters estimated
Rogers' index at day t (I_t)	Associated parameters of $\beta_{0,t}$, $\beta_{1,t}$, and σ_t^2	Normal (eq. 1) = L_1	Unknown total return size ($\bar{r}_{\cdot,\cdot}$)
No	Total return sizes of years i ($\bar{r}_{\cdot,i}$) since 1985; Rogers' indices at day t of years i ($I_{t,i}$) since 1985	Normal (eq. 2)	Three parameters ($\beta_{0,t}$, $\beta_{1,t}$, and σ_t^2) associated in the first likelihood function, L_1
Age composition of the Port Moller test fishery catches ($U_{a,i}$, where a = 1, 2, 3, 4)	Associated parameters of G_1, G_2, and G_3	Multinomial (eq. 5) = L_2	Unknown four-age return sizes combined across fishing districts ($\bar{r}_{a,i}$)
No	Four-age return sizes in years i ($\bar{r}_{a,i}$, where a = 1, 2, 3, 4) since 1985; four-age catches of the Port Moller test fishery in years i ($M_{a,i}$) since 1985	Multinomial (eq. 6)	Three parameters (G_1, G_2, and G_3) associated in the second likelihood function, L_2
Stock-specific return size up to day t ($U_{s,t}$) updates $\mu_{s,t}$ and $\delta_{s,t}^2$	Ten associated parameters of $\mu_{s,t}$ and $\delta_{s,t}^2$, where s = 1, 2,..., 5	Lognormal (eq. 8) per stock. For five stocks, $\prod_{s=1}^{5}(L \text{ of eq. } 8) = L_3$	Unknown stock-specific return size ($\bar{r}_{s,\cdot}$, where s = 1, 2, ..., 5)
Stock-specific return size up to day t ($U_{s,t}$, where s = 1, 2,..., 5)	Stock-specific return proportions by day t in years i ($h_{s,t,i}$) since 1955, except for the Togiak stock, which started in 1958	Lognormal (eq. 9) per stock. For five stocks, five lognormal likelihood functions (eq. 9)	Ten parameters ($\mu_{s,t}$ and $\delta_{s,t}^2$, where s = 1, 2, ..., 5) associated in the third likelihood function, L_3
Four-age return sizes per stock up to day t ($U_{s,a,t}$, where s = 1, 2, ..., 5 and a = 1, 2, 3, 4)	No	Multinomial (eq. 12) per stock. For five stocks, $\prod_{s=1}^{5}(L \text{ of eq. } 12) = L_4$	Unknown four-age return sizes per stock ($\bar{r}_{s,a}$, where s = 1, 2, ..., 5 and a = 1, 2, 3, 4)

rameters of models derived from previous years' data. There is a likelihood of the in-season observations given the parameters derived from previous years data, and there is a likelihood of the parameters given previous years' data. For management purposes, these parameters are of no real interest, but we treat them in a fully Bayesian way, allowing for full uncertainty. For instance, the Rogers' Port Moller index approach is a regression between cumulative catch index to date and the total return for the year. The two likelihood components are (*i*) the likelihood of this year's total return given the index-to-date and the parameters of the regression and (*ii*) that of the parameters of the regression given the historical data on total returns and index-to-date.

Each day of the fishing season is treated independently in that the same preseason prior information is used, and the cumulative data up to that day are used to calculate likelihoods. A list of the notations used in developing the model is provided in Appendix A, Table A1. The data available used in our calculations fall into two groups: those data collected in-season and those data from previous seasons.

Likelihood function of total return size based on Rogers' Port Moller index

Rogers' Port Moller index provides an estimate of the total return to Bristol Bay for the year based on the cumulative index of fish caught in the Port Moller fishery up to any date. The total return is simply the sum of the 20 individual age/district predicted returns. We used a first-order linear regression model for the likelihood function of total return size, where its explanatory variable was the cumulative Rogers' index up to a specified day t (I_t) during the Port Moller test fishery (Rogers 1994; Rogers and Steen 2000). It was assumed that total return size was normally distributed, i.e., $\bar{r}_{\cdot,\cdot} \sim N(E(\bar{r}_{\cdot,\cdot}),\sigma_t^2)$, where $E(\bar{r}_{\cdot,\cdot}) = (\beta_{0,t} + \beta_{1,t} I_t)$.

Equation 1 is the normal likelihood function of unknown total return size, ignoring constants:

$$(1) \qquad L(\bar{r}_{\cdot,\cdot}) \propto \exp\left[-\frac{[\bar{r}_{\cdot,\cdot} - (\beta_{0,t} + \beta_{1,t} I_t)]^2}{2\sigma_t^2}\right]$$

where the expected value of unknown total return size $\bar{r}_{\cdot,\cdot}$ is $\beta_{0,t} + \beta_{1,t} I_t$ and its variance is σ_t^2. This likelihood function is the first likelihood function in our forecast model components (i.e., $L(\bar{r}_{\cdot,\cdot}) \equiv L_1$; Table 1, Fig. 3*a*). Because $\bar{r}_{\cdot,\cdot} = \sum_{s=1}^{5}\sum_{a=1}^{4}\bar{r}_{s,a}$, we can also consider this likelihood function as a function of 20 variables, i.e.,

$$L(\bar{r}_{\cdot,\cdot}) = L\left(\sum_{s=1}^{5}\sum_{a=1}^{4}\bar{r}_{s,a}\right) \equiv L_1$$

The parameters σ_t^2, $\beta_{0,t}$, and $\beta_{1,t}$ are additional parameters of our model, and the joint likelihood function of those three parameters is shown in eq. 2 reflecting the relationship between the index up to a specific day and the total return for that year (Table 1):

$$(2) \qquad L(\beta_{0,t},\beta_{1,t},\sigma_t^2) \propto \prod_{i=1}^{n}\frac{1}{\sqrt{\sigma_t^2}}\exp\left\{-\frac{[\bar{r}_{\cdot,i} - (\beta_{0,t} + \beta_{1,t} I_{t,i})]^2}{2\sigma_t^2}\right\}$$

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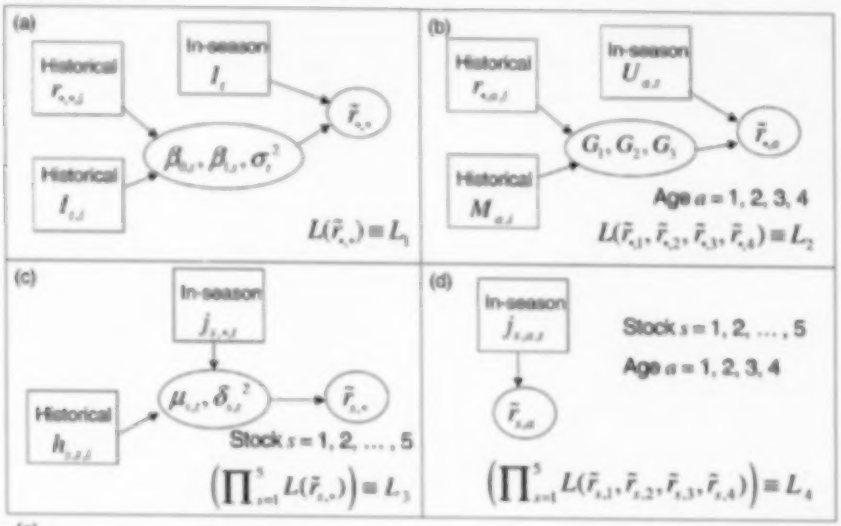
Fig. 3. Directed acyclic graph showing the calculation sequence. Rectangular nodes are fixed quantities and elliptical nodes are stochastic quantities. The arrows represent stochastic links where the target is a stochastic value with distribution depending on the values of the quantities in the source nodes. (*a*) Calculation sequence for the first likelihood function L_1 (eq. 1), where associated parameters $\beta_{0,t}$, $\beta_{1,t}$, and σ_t^2 are calculated with historical data of total return sizes ($r_{\cdot,\cdot,i}$) and Rogers' indices ($I_{t,i}$). Estimates of those associate parameters and in-season data of Rogers' indices (I_t) are then used for the calculation of unknown total return sizes ($\tilde{r}_{\cdot,\cdot}$). (*b*) Calculation sequence for the second likelihood function L_2 (eq. 5), where associated parameters G_1, G_2, and G_3 are calculated with historical data of four-age return sizes ($r_{\cdot,a,i}$) and four-age catches of the Port Moller test fishery ($M_{a,i}$). Estimates of those associated parameters and in-season data of cumulative four-age catches ($U_{a,t}$) are then used for the calculation of unknown four-age return sizes combined across fishing districts ($\tilde{r}_{\cdot,a}$). (*c*) Calculation sequence for the third likelihood function $L_3 = \prod_{s=1}^{5}(L \text{ of eq. 8})$, where associated parameters $\mu_{s,t}$ and $\delta_{s,t}^2$ are calculated with historical data of stock-specific return proportions by day ($h_{s,\cdot,i}$) and in-season data of stock-specific return size up to a day ($j_{s,\cdot,t}$). Estimates of those associate parameters are then used for the calculation of unknown stock-specific return size ($\tilde{r}_{s,\cdot}$). (*d*) Calculation sequence for the fourth likelihood function $L_4 = \prod_{s=1}^{5}(L \text{ of eq. 12})$, where in-season data of four-age return sizes per stock up to a day ($j_{s,a,t}$) are used for the calculation of unknown four-age return sizes per stock ($\tilde{r}_{s,a}$). (*e*) In the integration stage, two kinds of prior were used: (*i*) uninformative and improper uniform prior (i.e., constant) and (*ii*) a normal density prior from information of preseason forecasts of returns.



where the constant term with respect to σ_t^2, $\beta_{0,t}$, and $\beta_{1,t}$ is ignored, $r_{\cdot,\cdot,i}$ is total return size in past year i, and $I_{t,i}$ is the cumulative Rogers' index at day t of the corresponding year i. In eq. 2, there is no tilde mark (~) for $r_{\cdot,\cdot,i}$ because it is observed data. The units of these parameters are as follows: $[\beta_{0,t}]$ = return size, $[\beta_{1,t}]$ = return size/Rogers' index, and $[\sigma_t^2]$ = (return size)^2. Values of these parameters are different for each day t.

Likelihood of age composition at Port Moller

Age composition of the test fishery catch generally matches that of the return during the run season when corrected for size-specific gillnet selectivity (Hyun 2002*a*). Thus, the age composition data from Port Moller provide information about the proportion at age for the Bristol Bay run as a whole. This is indeed the primary motivation for operating the Port Moller test fishery. We used the age composition of the Port Moller fishery catch to develop a probability distribution for the age composition of returns to all of Bristol Bay. The joint probability of age-specific catches is multinomial (i.e., $\boldsymbol{U}_t \sim \text{Multinomial}(U_{\cdot,t}, \boldsymbol{P}_t)$, where $\boldsymbol{U}_t = (U_{1,t}, U_{2,t}, U_{3,t}, U_{4,t})$, $U_{\cdot,t} = \sum_{a=1}^{4} U_{a,t}$, and $\boldsymbol{P}_t = (P_{1,t}, P_{2,t}, P_{3,t}, P_{4,t})$). The $U_{a,t}$ is the cumulative number of age a fish caught by the Port Moller fishery up to day t, and $P_{a,t}$ is the proportion of age a fish out of the cumulative Port Moller catch up to day t.

By definition, the multinomial probability function becomes the likelihood function of the parameters, which are age-specific proportions, i.e., $p(\boldsymbol{U}_t|\boldsymbol{P}_t) = L(\boldsymbol{P}_t|\boldsymbol{U}_t)$. Equation 3 is the multinomial likelihood function ignoring constants:

$$(3) \qquad L(P_{1,t}, P_{2,t}, P_{3,t}, P_{4,t}) \propto \prod_{a=1}^{4} (P_{a,t}^{U_{a,t}})$$

To make this likelihood in eq. 3 have return sizes as variables, we reparameterized $P_{a,t}$ as in eq. 4:

$$(4) \qquad P_{a,t} = \frac{U_{a,t}}{\sum_{a=1}^{4} U_{a,t}} = \frac{\tilde{r}_{\cdot,a} G_a}{\sum_{a=1}^{4} (\tilde{r}_{\cdot,a} G_a)}$$

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where G_a is the fishery relative selectivity for age a fish. The G_a does not have a time subscript because it is constant by year and day unless mesh size of the fishing gear changes (Helton 1991).

Replacing $P_{a,i}$ in eq. 3 with $\overline{r}_{a,i}$ based on the reparameterization of eq. 4, we have the joint likelihood function of unknown age-specific return sizes:

$$(5) \qquad L(\boldsymbol{P}_i) \propto \prod_{a=1}^{4}\left(\frac{\overline{r}_{a,i}G_a}{\sum_a(\overline{r}_{a,i}G_a)}\right)^{U_{a,i}} = L(\overline{r}_{1,i},\overline{r}_{2,i},\overline{r}_{3,i},\overline{r}_{4,i})$$

In eq. 5, we ignored the constant term with respect to age-specific return sizes ($\overline{r}_{1,i},\overline{r}_{2,i},\overline{r}_{3,i},\overline{r}_{4,i}$). The $U_{a,i}$ is an age-specific catch of the Port Moller test fishery that is observed during the season. The likelihood function of eq. 5 is changed by $U_{a,i}$ being updated daily during the season. We designated the likelihood function of eq. 5 the second likelihood function, i.e., $L(\overline{r}_i) \equiv L_2$ (Table 1; Fig. 3*b*). This likelihood function can be expressed as that of 20 variables because $\overline{r}_{5,a} = \sum_{s=1}^{5}\overline{r}_{s,a}$, i.e.,

$$L(\overline{r}_{1,i},\overline{r}_{2,i},\overline{r}_{3,i},\overline{r}_{4,i}) = L\left(\sum_{s=1}^{5}\overline{r}_{s,1},\sum_{s=1}^{5}\overline{r}_{s,2},\sum_{s=1}^{5}\overline{r}_{s,3},\sum_{s=1}^{5}\overline{r}_{s,4}\right) \equiv L_2$$

For the values of associated parameters $\boldsymbol{G}$, the joint likelihood function depends on the historical data on total bay-wide returns and the catch at age at Port Moller (Table 1; Fig. 3*b*):

$$(6) \qquad L(G_1,G_2,G_3) \propto \prod_{i=1}^{n}\prod_{a=1}^{4}\left[\frac{r_{a,i}G_a}{\sum_a(r_{a,i}G_a)}\right]^{M_{a,i}}$$

where G_4 equals 1 and the constant term with respect to $\boldsymbol{G}$ is ignored. The $r_{a,i}$ is age-specific return size in past year i, and $M_{a,i}$ is the total age-specific catch from the Port Moller fishery in the corresponding year i (i.e., the cumulative number of age a fish caught by the Port Moller fishery up to the last day of the fishery). The gillnet gear selectivity for age 2.3 fish was assumed to be maximal (i.e., $G_4 = 1$) because at this age, the fish are most vulnerable to the gillnet mesh. Note again that there is no tilde mark for $r_{a,i}$ because it is observed data. The unit of G_a is a fraction whose range is from 0 to 1.

Likelihood function of return size for different stocks

For each stock for each day, the cumulative return size (catch plus escapement) is known. When catch and escapement to date are high relative to the long-term average, they generally indicate a larger run, although this is confounded by year-to-year differences in run timing. A large cumulative catch and escapement may be due to the run being early rather than large.

The data used to develop the likelihood function of unknown stock-specific return size came from two sources: (*i*) observed cumulative return size of a stock up to a specified day during the season and (*ii*) historical cumulative return proportion of the stock up to a specified day. Final return size was calculated by dividing the observed cumulative return size by the proportion. However, the return proportion on the specified days was highly variable (Fig. 2), so we used all of the historical return proportions rather than the mean value of the proportions:

$$(7) \qquad r_{s,i} = \frac{j_{s,i,i}}{\boldsymbol{h}_{s,i}}$$

where $\boldsymbol{h}_{s,i} = \{h_{s,i,i} | i = \text{years } 1, 2, \ldots, n\}$

In eq. 7, the numerator is a scalar but the denominator is a vector. We considered a histogram of these values ($\boldsymbol{r}_{s,i} = \{r_{s,i,i} | i = 1, 2, \ldots, n\}$) as a distribution for stock-specific return size. For example, the distribution of the 1999 Egegik return size calculated on 24 June, 30 June, 6 July, 12 July, 18 July, and 24 July is shown in Fig. 4. The variance of the distribution is small during the initial and final stages of the season (24 June and 24 July), whereas it is large in the middle of the season.

For a parametric description of the distribution of unknown return size generated from eq. 7, we explored various parametric likelihood functions for the distribution of $\boldsymbol{r}_{s,i}$. Using the Kolmogorov–Smirnov goodness-of-fit test, we found that the appropriate parametric likelihood was lognormal, i.e., $\overline{r}_{s,i} \sim \text{lognormal}(\mu_{s,i}, \delta^2_{s,i})$.

The lognormal likelihood function of unknown stock-specific return size $\overline{r}_{s,i}$ is

$$(8) \qquad L(\overline{r}_{s,i}) \propto \frac{1}{\overline{r}_{s,i}}\exp\left[-\frac{(\ln\overline{r}_{s,i}-\mu_{s,i})^2}{2\delta^2_{s,i}}\right]$$

where constants are ignored. The lognormal likelihood function of eq. 8 is changed by $\mu_{s,i}$ and $\delta^2_{s,i}$ and is updated daily during the season (Fig. 3*c*).

An independent likelihood function was developed for each of the five stocks. We assumed that the respective likelihood functions of the five stocks were independent because the spawning grounds are clearly separated (Fig. 1), stock run size and timing differ, and Alaska Department of Fish and Game manages each of the stocks as an individual entity (Minard and Meacham 1987). Thus, the joint likelihood function of five stock-specific returns is the product of the respective likelihood function. We designated this joint likelihood function the third likelihood function (i.e., $L(\overline{r}_{1,i},\overline{r}_{2,i},\ldots,\overline{r}_{5,i}) = \prod_{s=1}^{5}L(\overline{r}_{s,i}) \equiv L_3$; Table 1, Fig. 3*c*). Also, we can consider L_3 as a function of 20 variables because

$$\overline{r}_{s,i} = \sum_a \overline{r}_{s,a}$$

That is

$$\prod_{s=1}^{5}L(\overline{r}_{s,i}) = \prod_{s=1}^{5}L\left(\sum_{a=1}^{4}\overline{r}_{s,a}\right) \equiv L_3$$

For the values of associated parameters $\mu_{s,i}$ and $\delta^2_{s,i}$, their joint likelihood function ignoring constants is (Fig. 3*c*)

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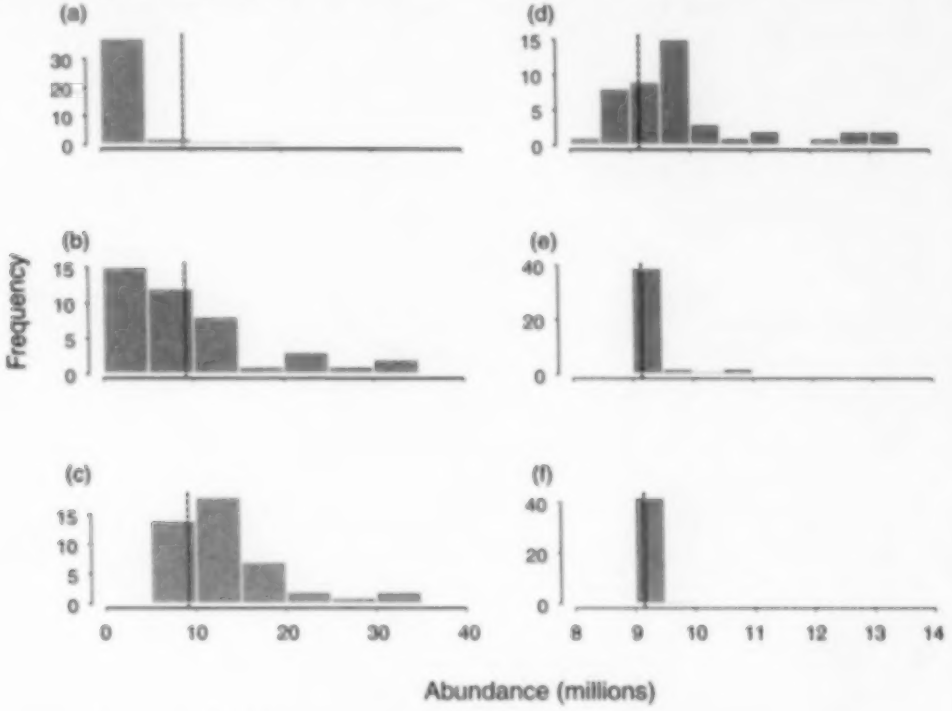
Fig. 4. Histogram for stock-specific return size calculated with eq. 7. The distribution of the 1999 Egegik sockeye salmon (*Oncorhynchus nerka*) return size is calculated at the specified day: (*a*) 24 June, (*b*) 30 June, (*c*) 6 July, (*d*) 12 July, (*e*) 18 July, and (*f*) 24 July. The vertical broken line is the actual return size.



$$(9)\qquad L(\mu_{s,t},\delta^2_{s,t}) \propto \prod_{i=1}^{n} \frac{1}{\sqrt{\delta^2_{s,t}}} \exp\left[-\frac{(\ln \overline{r}_{s,i,t}-\mu_{s,t})^2}{2\delta^2_{s,t}}\right]$$

where $r_{s,i,t}$ is an ith element (historical years) out of the return sizes for stock s, which are calculated using eq. 7. The units of $\mu_{s,t}$ and $\delta^2_{s,t}$ are as follows: $[\mu_{s,t}]$ = ln(return size) and $[\delta^2_{s,t}] = [\ln(\text{return size})]^2$. The estimation of $\mu_{s,t}$ and $\delta^2_{s,t}$ involves not only historical data ($h_{s,t,i}$) but also in-season data ($j_{s,a,t}$) (Fig. 3*c*). Estimates of $\mu_{s,t}$ and $\delta^2_{s,t}$ are different at day t. Since there were two parameters of $\mu_{s,t}$ and $\delta^2_{s,t}$ associated in the lognormal likelihood function for each stock, we had 10 associated parameters (i.e., five pairs) for five stocks.

Likelihood of the age composition of catch and escapement for each stock

The catch and escapement for each stock are sampled for age composition and this provides the best data about the relative strength of the age groups returning to each stock. We modeled the joint probability distribution of observed four-age return sizes to each district to a specified date with a multinomial probability function. The principle of the multinomial model is the same as that used to develop the joint likelihood function of four-age return sizes. By definition, the multinomial probability function of observed four-age return sizes is the likelihood function of the parameters, which are age-specific proportions per stock, i.e., $p(\boldsymbol{j}_{s,t} \mid \boldsymbol{R}_{s,t}) = L(\boldsymbol{R}_{s,t} \mid \boldsymbol{j}_{s,t})$. Equation 10 is the likelihood function ignoring constants:

$$(10)\qquad L(R_{s,1,t}, R_{s,2,t}, R_{s,3,t}, R_{s,4,t}) \propto \prod_{a=1}^{4} R_{s,a,t}^{j_{s,a,t}}$$

where $R_{s,a,t}$ is the proportion of age a fish out of the cumulative return to district s up to day t and $j_{s,a,t}$ is the observed cumulative return of stock s and age a up to day t.

Similar to the joint likelihood function of four-age return sizes calculation, we reparameterized $R_{s,a,t}$ to make the likelihood of eq. 10 have unknown return sizes as variables. We reparameterized it as follows:

$$(11)\qquad R_{s,a,t} = \frac{j_{s,a,t}}{\sum_{a} j_{s,a,t}} = \frac{\overline{r}_{s,a}}{\sum_{a} \overline{r}_{s,a}}$$

In the above case, we did not consider the fishery selectivity for age-specific fish because return data came from escapement counts as well as the gillnet fishery and research beach seines, so the age composition data for a stock should represent the total return, despite any selectivity in the gillnet fishery.

Expressing the likelihood function in eq. 10 by unknown four-age return sizes per stock ($\overline{r}_{s,1}, \overline{r}_{s,2}, \overline{r}_{s,3}, \overline{r}_{s,4}$) in eq. 11 gives

$$(12)\qquad L(\boldsymbol{R}_{s,t}) \propto \prod_{a=1}^{4} \left(\frac{\overline{r}_{s,a}}{\sum_{a} \overline{r}_{s,a}}\right)^{j_{s,a,t}} = L(\overline{r}_{s,1}, \overline{r}_{s,2}, \overline{r}_{s,3}, \overline{r}_{s,4})$$

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where we ignored the constant term with respect to $(\overline{r}_{s,1}, \overline{r}_{s,2}, \overline{r}_{s,3}, \overline{r}_{s,4})$. This likelihood function of eq. 12 is changed by $j_{s,a,t}$ updated everyday during the season. Again, because there are five stocks, we had to consider five likelihood functions. Owing to the independence of the five stocks,

$$L(\overline{r}_1, \overline{r}_2, \ldots, \overline{r}_5) = \left(\prod_{s=1}^{5} L(\overline{r}_s) \right)$$

We designated this function the fourth likelihood function, i.e.,

$$\prod_{s=1}^{5} L(\overline{r}_s) = L_4$$

(Table 1; Fig. 3*d*). This likelihood function is also a function of 20 variables, i.e.,

$$\prod_{s=1}^{5} L(\overline{r}_{s,1}, \overline{r}_{s,2}, \overline{r}_{s,3}, \overline{r}_{s,4}) = L_4$$

Prior: preseason forecasts of return sizes

Preseason return size forecasts are only available information before fish return season. We used preseason forecasts as a prior in a Bayesian framework following Fried and Hilborn (1988). UW ASP linear regression models predict fish returns by district and by age using run size and estimates of numbers of fish at earlier life stages (e.g., the approaching run, immature fish at sea, seaward migrant smolt, fry in lakes, or the number of spawners) (Rogers 1994). However, neither UW ASP nor the Alaska Department of Fish and Game provides variances for preseason forecasts. Based on the historical performance of preseason forecasts, we applied a wide variance to variances of preseason forecasts to cover the poor performance. The coefficient of variation (CV = SD/mean) of 3.0 was wide enough to cover the poor performance.

We assumed that preseason forecasts of district- and age-specific returns were normally distributed (eq. 13). Returns of the five stocks were independent, and further, it was reasonable to assume that returns of the four ages within each stock are independent because they are not siblings. This independence means the joint probability density of returns is the product of the respective densities of returns. That is, the joint normal density of $\overline{r}$ ignoring constants is expressed as

$$(13) \qquad p(\overline{r}) \propto \prod_{s} \prod_{a} \exp\left(-\frac{[\overline{r}_{s,a} - E(\overline{r}_{s,a})]^2}{2\mathrm{Var}(\overline{r}_{s,a})} \right)$$

where $\overline{r} = (\overline{r}_{1,1}, \overline{r}_{1,2}, \overline{r}_{1,3}, \ldots, \overline{r}_{5,3}, \overline{r}_{5,4})$. $E(\overline{r}_{s,a})$ is preseason forecast (point estimate) of stock s and age a return size made by UW ASP, and $\mathrm{Var}(\overline{r}_{s,a}) = [\mathrm{CV\ of\ 3.0} \times E(\overline{r}_{s,a})]^2$. This probability density of eq. 13 remains the same during the season. Equation 13 also is a function of 20 variables, i.e., $p(\overline{r}) = p(\overline{r}_{1,1}, \overline{r}_{1,2}, \overline{r}_{1,3}, \ldots, \overline{r}_{5,3}, \overline{r}_{5,4})$.

Integration

The respective likelihood functions are summarized in Table 1, and the flow of calculations in the algorithm is shown in Fig. 3. When we calculated unknown return sizes and associated parameters (Fig. 3), we took negative logarithms of the corresponding likelihood functions to easily differentiate them with respect to variables in the respective functions. Using Bayes' law, we integrated the likelihood and prior functions and calculated modes (point estimates) of return sizes and their associated credible intervals such as highest posterior density (HPD) regions. Because of differences between Bayesianism and frequentism, we avoid the term "confidence interval".

Bayesian framework

Equation 14 expresses Bayes' law, where a denominator constant term on the right side was ignored. The $p(\overline{r}|\mathrm{data})$ represents the joint posterior density of unknown stock- and age-specific returns $(\overline{r}_{1,1}, \overline{r}_{1,2}, \overline{r}_{1,3}, \ldots, \overline{r}_{5,3}, \overline{r}_{5,4})$. $L(\overline{r}|\mathrm{data})$ is the joint likelihood function of those returns, and $p(\overline{r})$ denotes the joint prior density. Calculation of the posterior density is updated daily in-season; it is changed by in-season data (Fig. 3*e*):

$$(14) \qquad p(\overline{r}|\mathrm{data}) \propto L(\overline{r}|\mathrm{data})\, p(\overline{r}) = [L_1 L_2 L_3 L_4]\, p(\overline{r})$$

The product of L_1, L_2, L_3, L_4, and $p(\overline{r})$ is based on the independence assumption. The $p(\overline{r})$ (preseason forecasts) is independent of the likelihood functions because preseason forecasts are made before the return season, and the data source is not from the season. The Port Moller catch data (L_1 and L_2) and the inshore return size data (L_3 and L_4) are independent samples. Further, the independence between the Port Moller catch (L_1) and its age composition (L_2) and that between the inshore return size (L_3) and its age composition (L_4) are true because age composition has nothing to do with the increase or decrease in catch and run size.

We used AD Model Builder (ADMB) software (Fournier 2000) to calculate the posterior density of 20 unknown return sizes in eq. 14. The Metropolis–Hastings algorithm of the Markov chain Monte Carlo (MCMC) calculation is implemented in ADMB (Gelman et al. 1995; Gamerman 1997). We performed 1 500 000 MCMC iterations, sampling the results at intervals of 1000 because of autocorrelation (Raftery and Lewis 1996; Patterson 1999). We discarded the first 50 000 samples as the burn-in period.

To check the convergence of MCMC samples, we used three indicators and also visually checked whether there are obvious patterns of lack of convergence. Those three indicators were (*i*) the Raftery and Lewis statistic, (*ii*) lag 1 autocorrelation, and (*iii*) the ratio between the time series standard deviation (based on an estimate of the spectral density at 0) and the naïve standard deviation (ignoring autocorrelation of the chain) (Raftery and Lewis 1992; Cowles and Carlin 1995; Brooks and Roberts 1998). A lack of convergence is indicated by a value for the dependence factor of the Raftery and Lewis statistic in excess of 5. The ratio between the two standard deviations should be around 1 if no autocorrelation is present.

We expressed uncertainty in return forecasts as the mode and approximate 95% HPD region of the posterior density. Because the posterior density is based on a frequency distribution of MCMC samples, statisticians cannot calculate an "exact" HPD region (Casella and Berger 1990; Gelman et al. 1995).

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Model performance

To evaluate model performance, we hindcasted stock-specific returns from early-season data from 24 June, 29 June, 4 July, and 9 July for the years 1999, 2000, and 2001. We compared posterior distributions of stock-specific returns with actual returns not included in the forecast model. In-season forecasts are made every day during the run season, but we chose these four days for demonstration purposes.

To evaluate the effects of various information combinations on forecasts, we calculated posterior distributions of return sizes using the following four information sets: information set I, inshore return data (catch and escapement by district) (i.e., posterior $\propto [L_3 L_4]$); information set II, Port Moller fishery data and inshore return data (i.e., posterior $\propto [L_1 L_2 L_3 L_4]$); information set III, inshore return data and preseason forecasts (i.e., posterior $\propto [L_3 L_4 p(\vec{r})]$); information set IV, Port Moller fishery data, inshore return data, and preseason forecasts (i.e., posterior $\propto [L_1 L_2 L_3 L_4 p(\vec{r})]$).

An uninformative and improper uniform prior (i.e., a constant) was used for the calculation with information sets I and II, whereas an informative and proper prior of preseason forecasts was used for that with information sets III and IV. The Port Moller data were used for L_1 and L_2, whereas the inshore return data were used for L_3 and L_4. Preseason forecasts were $p(\vec{r})$. We did not consider the combination of Port Moller data and preseason forecasts because forecasts from those two sources are poor.

Results

Diagnosis of posterior MCMC samples

We evaluated 240 posterior distributions of stock returns (summed across the four age groups for a stock): forecasts of five stock returns at four days (24 June, 29 June, 4 July, and 9 July) with four information sets across all three years 1999, 2000, and 2001 (i.e., $240 = 5 \times 4 \times 4 \times 3$). Of these 240 cases, only 11 posterior distributions did not satisfy the diagnosis tests for MCMC samples' convergence. Those 11 posterior distributions were forecasts of 1999 Naknek–Kvichak return at 24 June made with information set I, of 1999 Egegik return at 24 June made with information set I, of 1999 Nushagak return at 24 June made with information set I, of 1999 Naknek–Kvichak return at 24 June made with information set IV, of 1999 Togiak return at 29 June made with information I, of 1999 Togiak return at 29 June made with information set II, of 2000 Nushagak return at 24 June made with information set I, of 2000 Nushagak return at 24 June made with information set IV, of 2000 Ugashik return at 4 July made with information set I, of 2001 Nushagak return at 29 June made with information set I, and of 2001 Ugashik return at 4 July made with information set I. We excluded these posterior distributions. The other posterior distributions were accepted because the Raftery and Lewis statistics for their MCMC samples were less than 5, the lag 1 autocorrelations were between –1 and 1, the ratios between the time series standard deviation and the naïve standard deviation were around 1, and also these distributions looked smooth and obviously unimodal.

Forecast performance as posterior distributions of stock-specific returns

We checked posterior distributions of stock-specific returns with actual returns whose values were not included in the forecast model. Forecasts made with combined information were obviously better than those by the individual information. In terms of the posterior marginal distributions' modes of stock returns that were built from four information sets early in the season (24 June, 29 June, 4 July, and 9 July), forecasts made from information sets II, III, and IV were much less biased than those from information set I, which is only inshore return data (Fig. 5).

However, in terms of the HPD region, forecasts made from information set II were best. The 95% HPD regions from information set II covered the actual return size most frequently (Fig. 5); out of the 229 cases that satisfied the diagnosis tests for the MCMC samples' convergence, the coverage frequency from information sets I, II, III, and IV was 34 out of 52 (=65.4%), 56 out of 59 (=94.9%), 49 out of 60 (=78.3%), and 47 out of 58 (=81.0%), respectively. Information sets I and II consist of only in-season data (inshore return and Port Moller fishery data) that are updated daily, whereas information sets III and IV also have preseason forecasts that remain constant during the season. Thus, the HPD regions from information sets I and II change with forecast day more obviously than those from information sets III and IV. The HPD regions from information sets I and II are wider than those from information sets III and IV because forecasts from information sets I and II are not restricted by preseason forecasts. Generally, the HPD region is small, large, and then gets smaller over forecast day (Fig. 5) because the variability in cumulative run proportion for each day is low, large, and then low (Fig. 2).

Discussion

Model validation

Likelihood function of total return size (L_1)

The regression (eq. 2) of total return and the cumulative Rogers' index to day was significant. For example, total returns in 1985–2001 (1986 data are missing) were significantly related to the cumulative Rogers' index up to 9 July in the same years: the determination coefficient (R^2) was 0.46 (p value = 0.004). Residuals of the regression model over forecast day are shown (Fig. 6). Residuals are reduced over forecast day (along the row in Fig. 6) as Rogers' index of the Port Moller data accumulate. When data from the poor forecast years of 1997 and 2001 were removed, the regression significance increased (right column in Fig. 6; $R^2 = 0.731$ and p value ≤ 0.001 at 4 July). Residuals have no particular pattern over year, so the regression model's variance is assumed constant over year. Autocorrelation is not a concern because the model (L_1) uses daily "updated" observed data. The regression model's residual autocorrelation parameters were also insignificant over lag (e.g., –0.20 to 0.32 over lag 1–4).

Nevertheless, the Rogers' index has proved since 1997 to be a poor predictor of run size, and Flynn and Hilborn (2004) provided an updated method for using the Port Moller data to predict total Bristol Bay returns. Incorporating the new

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Fig. 5. Modes and bounds of approximate 95% highest posterior density (HPD) regions in posterior marginal distributions of the 1999, 2000, and 2001 stock-specific return sizes (in millions) of sockeye salmon (*Oncorhynchus nerka*) to Bristol Bay, Alaska. The forecast results are arranged by year (column) and stock (row). Symbols +, ▲, ×, and ■ denote modes of forecasts made from information sets I, II, III, and IV, respectively, and the respective bars on the symbols indicate the bounds of approximate 95% HPD regions in the forecasts from the corresponding information sets. The horizontal broken line in each plot represents the actual return size. Missing bars or symbols are due to the forecast bounds and modes being located beyond the *y*-axis limit or because the posterior Markov chain Monte Carlo (MCMC) samples' lack of convergence was excluded.

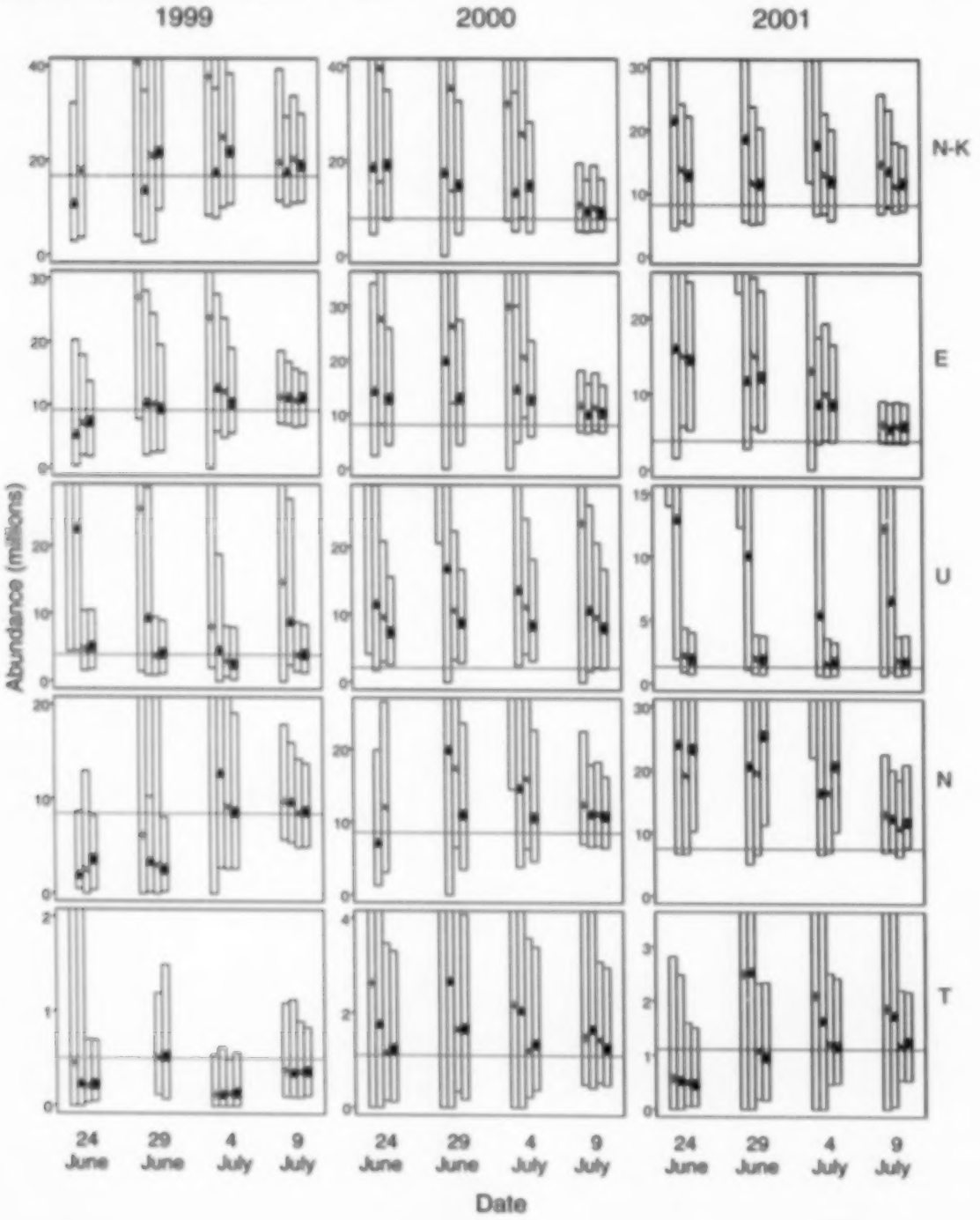

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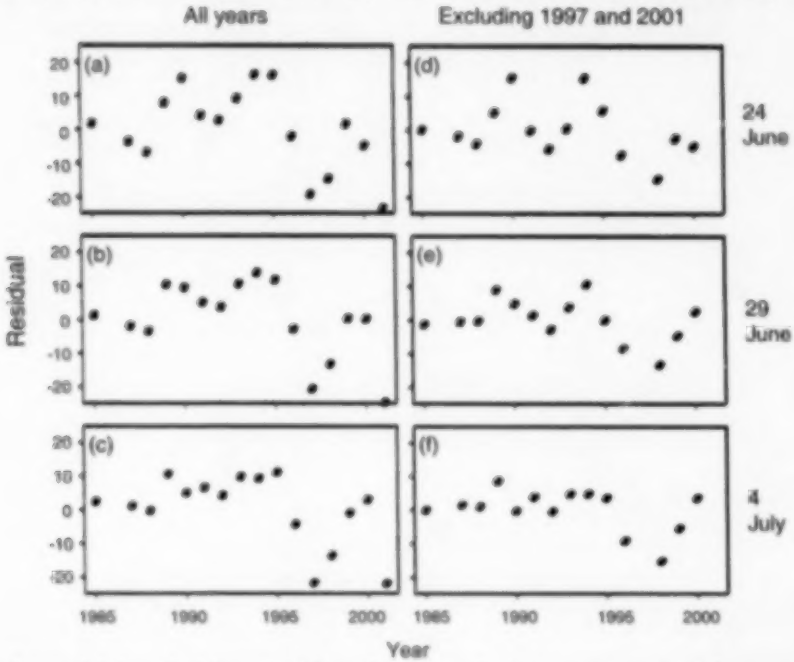
Fig. 6. Residuals over time from the Port Moller forecast model (L_1). When data from all available years were used: (*a*) $R^2 = 0.140$ and p value = 0.154 at 24 June, (*b*) $R^2 = 0.235$ and p value = 0.057 at 29 June, and (*c*) $R^2 = 0.330$ and p value = 0.020 at 4 July. Data from 1986 were not available because the Port Moller test fishery was not deployed in that year. When data from 1997 and 2001 were excluded, (*d*) $R^2 = 0.522$ and p value = 0.003 at 24 June, (*e*) $R^2 = 0.721$ and p value ≤ 0.001 at 29 June, (*f*) $R^2 = 0.731$ and p value ≤ 0.001 at 4 July.



Port Moller index in the model described here would possibly improve performance.

Joint likelihood function of four-age return sizes (L_2) and joint likelihood function of four-age return sizes per stock (L_4)

Using a multinomial mass function for the joint probability of multiple samples, four-age catches in this case, has the advantage of allowing unknown return sizes to become variables in the multinomial likelihood functions (L_2 and L_4) through reparameterization (eqs. 4 and 11). However, determining the appropriate sample sizes in the multinomial likelihood functions $\sum_{a=1}^{4} U_{a,t}$ in eq. 4 and $\sum_{a=1}^{4} j_{s,a,t}$ in eq. 11 was problematic owing to the assumption that an age composition probability distribution from fisheries data is a multinomial distribution. Sampling design and selection protocols usually generate estimates of age composition that necessarily depart to some degree from a strictly theoretical multinomial distribution (Fournier and Archibald 1982; Crone and Sampson 1998). Since the expanse and dynamics of fisheries prevent sampling in a strictly random manner, Crone and Sampson (1998) advised scaling down the actual catch size in a multinomial probability to avoid overweighting the multinomial likelihood function, e.g., L_2 or L_4 in our model. To determine optimum sample size, Crone and Sampson (1998) used weighted nonlinear regression analysis with the actual variance measures (e.g., CV) associated with the sample estimates (proportions) of age composition. However, owing to an absence of data, we set sample size by trial and error and found that any value of sample size smaller than 60 produced the same results. Indeed, our approach is a common technique practiced in fish stock assessment in dealing with a multinomial likelihood function.

Likelihood function of stock-specific return size (L_3)

For a parametric description of the distribution of stock-specific return size generated from eq. 7, we explored various parametric densities: normal, gamma, lognormal, and inverse Gaussian (Wald) (Hyun 2002*a*). Using the Kolmogorov–Smirnov goodness-of-fit test, the appropriate parametric density was lognormal or inverse Gaussian (p value ≅ 0.245–0.581; Hyun 2002*a*). Since the lognormal density shape was almost identical to that of the inverse Gaussian density, we did not distinguish between them. We selected the lognormal density, as it is more common than the inverse Gaussian density and thus is implemented in most statistical software.

Bayesian methods

We used UW ASP preseason forecasts of stock and age returns as prior information. UW ASP's preseason forecasts are based on significant linear regression models between numbers of fish in a run and estimates of the numbers of fish at earlier times in their life. Because only point estimates as preseason forecasts were provided, we applied wide variances (CV of 3.0) to cover possible poor forecasts. Preseason forecasts sometimes are seriously biased; absolute values of relative errors in preseason forecasts (point estimates) of 2000 returns ranged from about 15% to about 130% (Appendix A, Table A3). We found that applying wide variances to preseason forecasts led to better forecasts with

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information sets III and IV than applying narrow variances. When multiplying the likelihood functions from in-season data by the prior of preseason forecasts, increasing the variances of the preseason forecast distributions increases the overlap between the in-season likelihood and preseason forecast distributions. This wide overlap is reasonable because of the high uncertainty in preseason forecasts. Autocorrelation is not an issue because preseason forecasts remain the same during the run season.

Bayesian methodology enables us to integrate various data sets and build a forecast probability distribution for return sizes. Setting a prior function in a Bayesian format (posterior = likelihood × prior) is subjective as long as it is independent of the likelihood function. We apply two kinds of prior: (*i*) uninformative and improper uniform prior to the calculation of posterior with information sets I and II (i.e., posterior = likelihood × constant prior) and (*ii*) informative normal prior of preseason forecasts to that with information sets III and IV (i.e., posterior = likelihood × normal prior of preseason forecasts). The former constant prior does not affect the likelihood part at all, and the posterior results are reflected only by the likelihood part. Obviously, the prior of preseason forecasts is independent of the likelihood function from in-season data, where the likelihood part changes every day as in-season data are updated during the run season. Fried and Hilborn (1988) also used preseason run information as prior.

It cannot be justified whether the normal probability density of preseason forecasts is an appropriate prior and has a CV of 3.0 (eq. 13) because preseason forecasts are provided as only point estimates and there is no information about precision of those point estimates. A lognormal or gamma density could be also used as an informative prior of preseason forecasts. However, distributions of these densities are similar to that of a normal density when run size is large. The similarity is not surprising when recalling the central limit theorem where the sum of any random variable approaches a normal random variable as the summation increases.

Because the informative prior is questionable, our forecast models also allow the absence of preseason forecast information. Forecasts made with information sets I and II do not include preseason forecast information. This flexibility obviously benefits managers because managers have a few choices.

Forecasts made with information set II were as good as those made with information sets III and IV in terms of forecast bias, and forecasts from information set II were best in terms of coverage of forecast HPD regions. The less reliable performance from information sets III and IV compared with information set II is due to poor preseason forecasts themselves rather than the choice of the normal probability density as a prior distribution. These results are consistent with the intent of the Bayesian approach that integrates all available information. Information set II has all available information from in-season, which leads to the best performance. Information set IV has "additional but questionable" information of preseason forecasts. Unless preseason forecasts are luckily good, forecasts from information sets III and IV are less reliable than those from information set II, especially as in-season data are accumulated during fish run season.

We checked the posterior distributions of returns by comparing them with actual returns that had not been used in the calculation process. The respective marginal posterior distributions obviously improved over day in-season; the modes approached the actual returns and the distributions became narrower. The improvement is because more data are accumulated as the season progresses.

Uncertainty in associated parameters in the likelihood functions

When we calculated posterior MCMC samples of returns (eq. 14), we used random samples of the respective associated parameters from the corresponding likelihood functions of eqs. 2, 6, and 9 rather than their point estimates, such as maximum likelihood estimates. Their respective marginal distributions are summarized in Appendix A, Table A2, in terms of mode and 95% HPD bounds. The posterior distribution is the same as the likelihood function when an improper uniform prior (i.e., a constant prior) is used. We included parameters for the Port Moller fishery selectivity for age-specific fish (G_a, where $a = 1, 2, 3$), but the inclusion did not significantly improve forecasts when compared with forecasts with those parameter being ignored.

Conclusions

Effective management demands accurate early-season return forecasts, but such forecasts are challenging owing to a lack of early in-season data and large variability in run timing. Early in the season, forecasts of stock returns from combined likelihood functions are more accurate than those from individual likelihood functions. Early-season management decisions for stocks should be based on forecasts from information sets II, III, and IV.

In the later half of the season (about 10 July), using only inshore return data (L_3) produces relatively accurate forecasts of stock-specific returns except for Ugashik and Togiak stock returns whose run timing is significantly later. The mean values of historical proportions of Ugashik and Togiak stock runs on 10 July are still 36.1% and 31.9%, respectively, whereas those of the other stock runs on that day are all above 70%. Also, year-to-year variability in historical proportions of Ugashik and Togiak stock runs on that day is large (CV = 0.533 and 0.346, respectively), whereas the CVs for the other stock runs are all below 0.2.

The model could be improved in three ways: (*i*) incorporate data from test fisheries in the fishing districts and in the rivers beyond the commercial fishing boundaries to estimate number of fish present and improve in-season forecasting, (*ii*) incorporate the new Port Moller index described in Flynn and Hilborn (2004), and (*iii*) explicit treatment of run timing as a parameter of the model may provide additional improvements. Early runs appear large when using average proportion by date, but late runs appear small. Hyun (2002*b*) developed a simple algorithm for forecasting fish return timing using the catch data of the Port Moller test fishery. The Port Moller return timing index detected on 29 June explained about 58% of the annual variation in true return timing. The incorporation of the Port Moller return timing index improved the accuracy of the return size forecasts.

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In this paper, we have demonstrated that the diverse information available for in-season forecasting in the Bristol Bay sockeye fishery can be unified to provide a statistically based estimate. This method can be applied to other salmon fisheries and any fishery where in-season forecasting is made based on pre- and in-season data.

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Appendix A

Tables A1, A2, and A3 follow.

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Table A1. Notations used in developing the model for in-season age-specific forecasts of sockeye salmon (*Oncorhynchus nerka*) returns to the Bristol Bay districts of Alaska.

Notation	Description
Indices	
s	Stock (district)-specific fish. Five stocks were considered: stock code 1, Kvichak–Naknek; stock code 2, Egegik; stock code 3, Ugashik; stock code 4, Nushagak; stock code 5, Togiak
a	Age. Four age groups were considered: age code 1, age 1.2; age code 2, age 1.3; age code 3, age 2.2; age code 4, age 2.3. A fish of age $x.y$ spent x winter(s) in fresh water after the fry stage and y winter(s) in the ocean
t	Day
i	Year
$r_{s,a}$	Return size of stock s and age a
$r_{s,\cdot}$	Stock-specific return size ignoring age: $r_{s,\cdot} = \sum_{a=1}^{4} r_{s,a}$
$r_{\cdot,a}$	Age-specific return size ignoring stock: $r_{\cdot,a} = \sum_{s=1}^{5} r_{s,a}$
$r_{\cdot,\cdot}$	Total return size. Sum of district- and age-specific return sizes: $r_{\cdot,\cdot} = \sum_{s=1}^{5}\sum_{a=1}^{4} r_{s,a}$
$\boldsymbol{r}_{\cdot}$	Vector of age-specific return sizes ignoring stock: $r_{\cdot,1}, r_{\cdot,2}, r_{\cdot,3}, r_{\cdot,4}$
$\boldsymbol{r}_{s}$	Vector of age-specific return sizes for stock s: $r_{s,1}, r_{s,2}, r_{s,3}, r_{s,4}$
$\boldsymbol{r}$	Vector of 20 stock- and age-specific return sizes: $r_{1,1}, r_{1,2}, \ldots, r_{5,3}, r_{5,4}$
~	To distinguish unknown return sizes from observed return sizes, we use a tilde mark (e.g., $\tilde{r}_{s,a}$ is unknown return size of stock s and age a that we want to calculate, whereas $r_{s,a}$ is observed return size as data)
Data	
$r_{\cdot,\cdot,i}$	Total return size in historical year i
$r_{\cdot,a,i}$	Age-specific return size ignoring stock in historical year i
$r_{s,\cdot,i}$	Stock-specific return size ignoring age in historical year i
$\boldsymbol{r}_{s,\cdot}$	Vector of stock-specific return sizes ignoring age in historical years: $\{r_{s,\cdot,i} \mid i = \text{years } 1, 2, \ldots, n\}$
$I_{t,i}$	Cumulative Rogers' index up to day t of historical year i
I_t	Cumulative Rogers' index up to day t during in-season
$U_{a,t}$	Cumulative number of age a fish caught by the Port Moller fishery up to day t during in-season. Also, $\boldsymbol{U}_t = (U_{1,t}, U_{2,t}, U_{3,t}, U_{4,t})$
$U_{\cdot,t}$	Cumulative catch of the Port Moller fishery up to day t during in-season. Also $U_{\cdot,t} = \sum_{a=1}^{4} U_{a,t}$
$M_{a,i}$	Total number of age a fish caught by the Port Moller fishery in historical year i (i.e., the cumulative number of age a fish caught by the Port Moller fishery up to the last day of the fishery)
$\boldsymbol{h}_{s,t}$	Cumulative proportions of return sizes of stock s up to day t in historical years: $\{h_{s,t,i} \mid i = \text{years } 1, 2, \ldots, n\}$
$j_{s,a,t}$	Observed cumulative return of stock s and age a up to day t during in-season. We caution readers not to be confused with the above return sizes, $r_{s,a}$. The $r_{s,a}$ indicates final return size, which is the cumulative return up to the end of the season
$j_{s,\cdot,t}$	Observed cumulative return of stock s up to day t during in-season: $j_{s,\cdot,t} = \sum_{a=1}^{4} j_{s,a,t}$
Parameter(s)	
$\tilde{\boldsymbol{r}}$	Vector of unknown 20 stock- and age-specific return sizes: $\tilde{r}_{1,1}, \tilde{r}_{1,2}, \ldots, \tilde{r}_{5,3}, \tilde{r}_{5,4}$
$\beta_{0,t}, \beta_{1,t}, \sigma_t^2$	Associated parameters in the normal likelihood of eq. 1
$P_{a,t}$	Proportion of age a fish out of the cumulative Port Moller catch up to day t during in-season. Also, $\boldsymbol{P}_t = (P_{1,t}, P_{2,t}, P_{3,t}, P_{4,t})$
G_a	Relative selectivity of the Port Moller gillnet fishery for age a fish. Also, $\boldsymbol{G} = (G_1, G_2, G_3, G_4)$, where $G_4 = 1$ by assumption
$\mu_{s,t}, \delta_{s,t}^2$	Associated parameters in the lognormal likelihood of eq. 8. These parameter estimates differ by stock and change as in-season data are updated. Thus, they have subscripts s and t
$R_{s,a,t}$	Proportion of age a fish out of the cumulative return to district s up to day t during in-season. Also, $\boldsymbol{R}_{s,t} = (R_{s,1,t}, R_{s,2,t}, R_{s,3,t}, R_{s,4,t})$

Note: Bold and italic font is used for a vector to distinguish it from a scalar.

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Table A2. Uncertainty in associated parameters in terms of modes and bounds of approximate 95% HPD regions in the respective posterior marginal distributions.

		24 June			29 June			4 July			9 July		
Year	Parameter	Low	Mode	Up	Low	Mode	Up	Low	Mode	Up	Low	Mode	Up
1999	$\beta_{0,t}$	8.27	23.20	38.13	−1.28	14.29	31.59	−0.66	12.73	32.82	0.13	18.61	35.24
	$\beta_{1,t}$	0.00	0.02	0.05	0.01	0.02	0.04	0.00	0.01	0.02	0.00	0.01	0.02
	σ_t^2	79.80	114.63	184.30	68.01	93.85	154.15	64.17	93.79	153.04	77.99	104.91	167.74
	G_1	0.13	0.50	0.98	0.13	0.50	0.98	0.13	0.50	0.98	0.13	0.50	0.98
	G_2	0.28	0.79	1.00	0.28	0.79	1.00	0.28	0.79	1.00	0.28	0.79	1.00
	G_3	0.20	0.67	0.98	0.20	0.67	0.98	0.20	0.67	0.98	0.20	0.67	0.98
	$\mu_{1,t}$	8.19	8.56	8.97	7.43	7.78	8.14	9.71	9.89	10.04	9.67	9.76	9.84
	$\mu_{2,t}$	6.43	6.80	7.14	8.11	8.41	8.72	9.32	9.47	9.60	9.19	9.26	9.32
	$\mu_{3,t}$	8.41	8.73	9.02	7.60	7.88	8.22	6.47	6.75	7.03	7.95	8.16	8.40
	$\mu_{4,t}$	6.52	6.97	7.39	6.53	6.93	7.30	9.04	9.21	9.44	8.97	9.05	9.12
	$\mu_{5,t}$	3.92	4.20	4.47	4.99	5.37	5.78	4.36	4.55	4.80	5.27	5.44	5.57
	$\delta_{1,t}^2$	1.04	1.68	2.60	0.96	1.46	2.33	0.20	0.31	0.49	0.05	0.08	0.13
	$\delta_{2,t}^2$	0.78	1.27	2.10	0.66	1.01	1.66	0.15	0.24	0.36	0.03	0.05	0.08
	$\delta_{3,t}^2$	0.58	0.90	1.40	0.61	0.93	1.48	0.54	0.86	1.35	0.36	0.57	0.87
	$\delta_{4,t}^2$	1.35	2.11	3.51	1.05	1.72	2.71	0.30	0.46	0.74	0.04	0.07	0.10
	$\delta_{5,t}^2$	0.30	0.54	0.94	0.73	1.28	2.25	0.26	0.45	0.74	0.12	0.19	0.33
2000	$\beta_{0,t}$	9.49	23.39	37.28	−0.82	13.00	31.42	−0.26	14.44	30.99	2.17	17.24	33.99
	$\beta_{1,t}$	0.00	0.02	0.04	0.01	0.02	0.03	0.00	0.01	0.02	0.00	0.01	0.02
	σ_t^2	84.38	105.69	169.63	65.77	86.84	136.02	65.38	85.83	133.54	80.40	101.93	150.38
	G_1	0.17	0.51	0.98	0.17	0.51	0.98	0.17	0.51	0.98	0.17	0.51	0.98
	G_2	0.30	0.79	1.00	0.30	0.79	1.00	0.30	0.79	1.00	0.30	0.79	1.00
	G_3	0.23	0.52	0.98	0.23	0.52	0.98	0.23	0.52	0.98	0.23	0.52	0.98
	$\delta_{1,t}$	11.09	11.47	11.89	10.27	10.63	10.98	9.51	9.66	9.83	8.98	9.05	9.14
	$\mu_{2,t}$	9.85	10.17	10.56	10.29	10.61	10.88	9.58	9.74	9.86	9.17	9.23	9.30
	$\mu_{3,t}$	8.53	8.85	9.12	9.25	9.54	9.81	9.07	9.37	9.64	8.33	8.58	8.77
	$\mu_{4,t}$	7.64	8.10	8.52	10.36	10.71	11.11	9.59	9.75	9.97	9.19	9.27	9.34
	$\mu_{5,t}$	6.37	6.65	6.96	6.75	7.16	7.54	6.68	6.91	7.16	6.74	6.89	7.04
	$\delta_{1,t}^2$	1.00	1.63	2.63	1.00	1.57	2.37	0.18	0.30	0.48	0.05	0.08	0.12
	$\delta_{2,t}^2$	0.90	1.40	2.27	0.65	1.00	1.63	0.15	0.23	0.37	0.03	0.05	0.07
	$\delta_{3,t}^2$	0.54	0.84	1.39	0.58	0.89	1.44	0.56	0.94	1.40	0.36	0.54	0.87
	$\delta_{4,t}^2$	1.49	2.21	3.67	1.13	1.69	2.72	0.31	0.46	0.70	0.04	0.07	0.10
	$\delta_{5,t}^2$	0.37	0.68	1.15	0.74	1.30	2.15	0.29	0.50	0.84	0.14	0.21	0.35
2001	$\beta_{0,t}$	10.40	22.29	35.36	2.82	15.39	29.23	3.90	16.74	29.57	4.66	19.19	32.40
	$\beta_{1,t}$	0.01	0.03	0.04	0.01	0.02	0.03	0.01	0.01	0.02	0.00	0.01	0.02
	σ_t^2	83.35	103.40	153.53	68.08	82.44	121.92	64.35	80.01	121.78	75.85	95.32	134.27
	G_1	0.16	0.57	0.98	0.16	0.57	0.98	0.16	0.57	0.98	0.16	0.57	0.98
	G_2	0.29	0.71	1.00	0.29	0.71	1.00	0.29	0.71	1.00	0.29	0.71	1.00
	G_3	0.22	0.56	0.98	0.22	0.56	0.98	0.22	0.56	0.98	0.22	0.56	0.98
	$\mu_{1,t}$	11.68	12.10	12.45	10.43	10.82	11.18	9.63	9.79	9.96	9.30	9.38	9.46

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Table A2 (*concluded*).

Year	Parameter	24 June			29 June			4 July			9 July		
		Low	Mode	Up	Low	Mode	Up	Low	Mode	Up	Low	Mode	Up
	$\mu_{2,j}$	10.17	10.53	10.86	9.44	9.75	10.04	8.75	8.89	9.03	8.51	8.56	8.63
	$\mu_{3,j}$	8.74	9.01	9.34	8.07	8.39	8.65	7.12	7.39	7.69	7.29	7.52	7.72
	$\mu_{4,j}$	10.91	11.38	11.81	10.33	10.71	11.10	9.51	9.71	9.91	9.19	9.27	9.33
	$\mu_{5,j}$	5.07	5.38	5.66	6.18	6.57	6.97	6.60	6.86	7.06	6.82	6.96	7.11
	$\delta^2_{1,j}$	1.13	1.74	2.81	1.01	1.58	2.44	0.20	0.31	0.48	0.05	0.08	0.12
	$\delta^2_{2,j}$	0.88	1.43	2.18	0.68	1.07	1.62	0.15	0.24	0.36	0.03	0.05	0.07
	$\delta^2_{3,j}$	0.55	0.87	1.39	0.62	1.00	1.47	0.62	0.97	1.46	0.36	0.55	0.86
	$\delta^2_{4,j}$	1.45	2.25	3.46	1.16	1.74	2.73	0.29	0.44	0.71	0.04	0.06	0.10
	$\delta^2_{5,j}$	0.33	0.63	1.15	0.72	1.18	2.04	0.31	0.49	0.81	0.13	0.21	0.34

Note: $\beta_{a,j}$, $\beta_{1,j}$, and σ^2_j are associate parameters in the first likelihood function, L_j; G_a ($a = 1, 2, 3$) are associate parameters of the gillnet gear selectivity in the second likelihood function, L_2, where $a = 1, 2, 3$ denotes age 1.3, and age 2.2, respectively. $\mu_{s,j}$ and $\delta^2_{s,j}$ ($s = 1, 2, ..., 5$) are associate parameters in the third likelihood function, L_3, where $s = 1, 2, ..., 5$ denotes Naknek–Kvichak, Egegik, Ugashik, Nushagak, and Togiak, respectively. The units of these parameter values below are as follows: $[\beta_{a,j}]$ = return size in millions; $[\beta_{1,j}]$ = return size in millions/Rogers' index in CPUE; $[\sigma^2_j]$ = (return size in millions)^2; $[G_a]$ = fraction that ranges from 0 to 1; $[\mu_{s,j}]$ = natural logarithm of return size in thousands; and $[\delta^2_{s,j}]$ = (natural logarithm of return size in thousands)^2.

Table A3. Relative errors of University of Washington Alaska Salmon Program preseason forecasts of sockeye salmon (*Oncorhynchus nerka*) returns to the Bristol Bay districts of Alaska.

Year	Stock	Forecast ($\times 10^3$)	Actual run ($\times 10^3$)	Error (%)
1999	N–K	17 700 000	16 763 000	5.6
	E	7 700 000	9 150 000	−15.8
	U	2 700 000	3 919 000	−31.1
	N	6 640 000	8 484 000	−21.7
	T	380 000	504 000	−24.6
2000	N–K	14 200 000	7 878 043	80.2
	E	11 400 000	8 137 718	40.1
	U	4 900 000	2 128 114	130.3
	N	6 200 000	8 545 112	−27.4
	T	940 000	1 105 470	−15.0
2001	N–K	6 800 000	8 170 269	−16.8
	E	5 300 000	3 830 735	38.4
	U	1 400 000	1 309 431	6.9
	N	7 800 000	7 473 115	4.4
	T	480 000	1 108 133	−56.7

Note: Negative and positive values of errors indicate under- and over-forecasts. N–K, Naknek–Kvichak; E, Egegik; U, Ugashik; N, Nushagak; T, Togiak.

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Resource requirements of *Asterionella formosa* and *Fragilaria crotonensis* in oligotrophic alpine lakes: implications for recent phytoplankton community reorganizations

Jasmine E. Saros, Timothy J. Michel, Sebastian J. Interlandi, and Alexander P. Wolfe

Abstract: A widespread increase in the relative abundances of *Asterionella formosa* and *Fragilaria crotonensis* has occurred in oligotrophic alpine lakes across the western United States. Previous investigations have suggested that enhanced atmospheric nitrogen (N) deposition is driving these shifts in diatom community structure; however, little information is available on N requirements of these taxa. We examined the distributions of these two taxa in relation to a variety of physicochemical parameters in a suite of lakes situated in the Beartooth Mountain Range (Montana–Wyoming, USA). We also conducted a series of nutrient enrichment experiments to assess the response of these taxa to changes in N, phosphorus (P), and silica (Si) supply. The distributions of both taxa were positively correlated with C:P, N:P, and Si:P seston ratios, revealing that these taxa are abundant when P availability is very low and the supply of N and Si are moderate to high. In the enrichment experiments, both taxa responded strongly to N additions, whereas P or Si enrichment alone had no effect. While these two taxa are indicative of P enrichment in temperate lakes, our results indicate that in these oligotrophic alpine lakes, N enrichment is driving their recent increase.

Résumé : Il s'est produit une augmentation généralisée des abondances relatives d'*Asterionella formosa* et de *Fragilaria crotonensis* dans les lacs alpins oligotrophes dans tout l'ouest des États-Unis. Des études antérieures ont proposé que la déposition atmosphérique accrue d'azote (N) explique ces modifications de la structure des communautés de diatomées, bien qu'on ait que peu d'information sur les besoins en azote de ces taxons. Nous avons examiné la répartition de ces deux taxons en fonction d'une gamme de variables physico-chimiques dans une série de lacs de la chaîne des monts Beartooth (Montana–Wyoming, É.-U.). Nous avons aussi mené une gamme d'expériences d'enrichissement de nutriments afin d'évaluer la réaction de ces taxons à des changements dans les apports de N, de phosphore (P) et de silice (Si). Les répartitions des deux taxons sont en corrélation positive avec les rapports C:P, N:P et Si:P du seston, ce qui indique que ces taxons sont abondants lorsque la disponibilité de P est très faible et que les apports de N et de Si sont moyens à élevés. Dans les expériences d'enrichissement, les deux taxons réagissent fortement à une addition de N, alors que des enrichissements de P et de Si seuls restent sans effet. Alors que ces taxons indiquent un enrichissement en P dans les lacs tempérés, nos résultats montrent que, dans les lacs alpins oligotrophes, c'est l'enrichissement en N qui explique leur prolifération récente.

[Traduit par la Rédaction]

Introduction

In alpine lakes in several regions of the world, sedimentary diatom profiles indicate that rapid shifts in diatom community structure have occurred over the past century (Psenner and Schmidt 1992; Wolfe et al. 2001; Saros et al. 2003). In alpine lakes of the western United States (see Fig. 1), a widespread shift in diatom assemblages has occurred, with *Asterionella formosa* and *Fragilaria crotonensis* replacing typical alpine diatom taxa (e.g., *Staurisirella* spp., *Aulacoseira* spp., and stelligeroid *Cyclotella* spp.) since the 1950s (see Fig. 2). Enhanced atmospheric N deposition has been invoked as the causal factor behind the increases in these diatoms. However, while

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J.E. Saros[1] **and T.J. Michel.** Department of Biology, University of Wisconsin – La Crosse, 1725 State Street, La Crosse, WI 54601, USA.
S.J. Interlandi. Department of Bioscience and Biotechnology, 32nd and Chestnut Streets, Drexel University, Philadelphia, PA 19104, USA.
A.P. Wolfe. Department of Earth and Atmospheric Sciences, University of Alberta, 1-13 ESB, Edmonton, AB T6G 2E3, Canada.

[1]Corresponding author (e-mail: saros.jasm@uwlax.edu).

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Table 1. Half-saturation constants (μmol) measured for three resources using populations isolated from alpine lakes of the Beartooth Mountains.

	N	P	Si
Staurosirella pinnata	0.003 (0.056)	0.0003 (0.005)	3.82 (1.09)
Asterionella formosa	0.041 (0.038)	0.0009 (0.003)	3.35 (3.38)
Fragilaria crotonensis	0.028 (0.063)	0.0008 (0.065)	0.78 (0.97)

Note: A lower half-saturation constant value indicates a lower requirement for that nutrient. *Staurosirella pinnata* is a historically abundant diatom in alpine lakes of the southern and central Rocky Mountains. Standard error estimates are indicated in parentheses (modified from Michel 2003).

both of these taxa are frequently reported in mesotrophic temperate lakes (Reavie and Smol 2001), information on their specific resource requirements, particularly for N, is relatively sparse.

In temperate lakes, where Si and P are typically considered the principal nutrients that regulate seasonal diatom succession (Reynolds 1984), *A. formosa* and *F. crotonensis* appear to have similar Si and P requirements, so much so that their R^* values (equilibrium resource availability) for these nutrients are essentially identical (Tilman 1981). Both are excellent P competitors but have relatively high Si requirements; thus, they can be abundant at times when Si:P supply ratios are relatively high (Tilman 1982; Kilham 1986; Interlandi et al. 1999). In addition, they are often found together, as predicted by the R^* rule (Tilman 1982). Both taxa are reported to increase with eutrophication in temperate systems (Lotter 1998), presumably owing to increased P loading and despite indications that both are excellent competitors for P. However, in Lake Michigan, populations of *F. crotonensis* also appear sensitive to N additions (Stoermer et al. 1978), implying either unresolved resource physiologies or the development of biogeographically distinct ecotypes.

The N requirements of these diatoms in alpine lakes remain unclear, as prior investigations either focused on Si and P requirements or did not isolate N as the causal factor in observed changes. Yang et al. (1996) found that both *A. formosa* and *F. crotonensis* increased in Kootenay Lake (British Columbia) when it was enriched simultaneously with N and P. In a lake of the Colorado Front Range, McKnight et al. (1990) found that calcium nitrate or sulfuric acid additions stimulated the growth of *A. formosa*; thus, the reason for the stimulation was unclear. The distributions of both taxa in Yellowstone Lake were positively correlated with total N (TN) : total P (TP) as well as total Si:TP ratios (Interlandi et al. 1999).

Michel (2003) measured the resource requirements of these two taxa in alpine lakes of the central Rocky Mountains (Beartooth Mountain Range). Both *A. formosa* and *F. crotonensis* had very low P requirements, similar to those of a typical alpine diatom taxon, but moderate N requirements (Table 1), suggesting that greater N availability is promoting the widespread increase in these two taxa. In an effort to decipher which factors are driving the observed diatom community shifts in alpine lakes of the western United States, we explored the distribution of *A. formosa* and *F. crotonensis* in a suite of lakes in the Beartooth–Absaroka Wilderness in relation to a variety of physicochemical parameters including dissolved nutrient concentrations as well as seston nutrient ratios. We also examined the response of both taxa in two sets of nutrient enrichment experiments. In the first set, whole lake water was enriched with N, P, or N + P. In the second set, manipulations consisted of the following nutrient supply ratios: high N:P, low N:P, high Si:P, and low Si:P. Our overarching objective is to reconcile diatom resource physiology with paleoecology as a rigorous methodology for the interpretation of sediment diatom stratigraphies.

Materials and methods

Site description

The Beartooth Mountain Range comprises much of the Absaroka–Beartooth Wilderness and is located on the southwest Montana – Wyoming border, directly adjacent to the northeast entrance of Yellowstone National Park (Fig. 1). There are over 600 permanent alpine lakes in this region whose watersheds are highly sensitive to atmospherically deposited N owing to sparse vegetation, shallow soils, and large expanses of unbuffered crystalline bedrock. As a result of the slow weathering rates, lakes in this region are highly dilute with generally low Si and P concentrations (Saros et al. 2003). The concentration of N in precipitation and surface waters, although increasing, has remained relatively low (<2 kg N·ha^{-1}·year^{-1} in precipitation and <10 μmol N·L^{-1} in surface waters; Saros et al. 2003); increased bulk precipitation rates over the past century (Western Regional Climate Center 2001) may have increased N loading to these lakes. Depending on elevation, lakes in this area are typically ice-free from mid-June – early July until mid- to late October.

Paleolimnological methods

The data displayed in Fig. 2 were determined using the methods outlined in Saros et al. (2003) and Wolfe et al. (2003). Briefly, organic sediments were collected from each lake with a modified K-B gravity corer (Glew 1989) and extruded in consecutive 0.5-cm increments in the field. The diatom species composition of each sample was determined by preparing slides from digested (30% H_2O_2) sediment samples. The processed samples were settled onto coverslips and mounted onto slides with Naphrax®. A minimum of 300 valves per slide was counted under oil immersion on a Nikon E400 Eclipse microscope (Nikon Inc., Melville, New York) with phase-contrast under oil immersion at 1000× magnification. Diatom taxonomy was based primarily on Krammer and Lange-Bertalot (1986–1991) and Camburn and Charles (2000).

The chronology of recent sediments was based on ^{210}Pb distillation and alpha spectrometry methods (modified from Eakins and Morrison 1978), and dates and sedimentation

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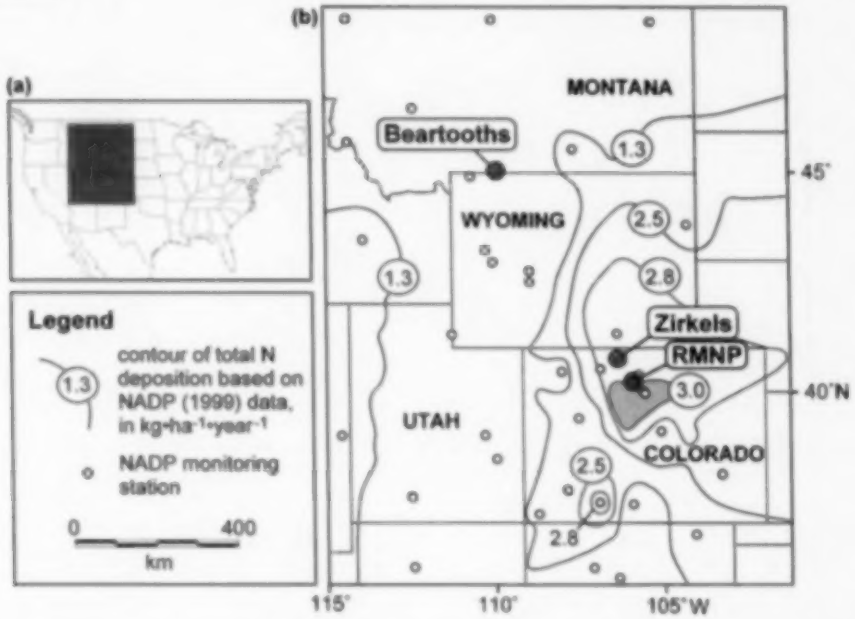
Fig. 1. Locations of three alpine regions of the western United States from which lacustrine sediment cores were collected: the Zirkel Wilderness and Rocky Mountain National Park (RMNP) of Colorado and the Beartooth Mountains of Montana and Wyoming. Data collected at these locations (National Atmospheric Deposition Program/National Trans Network 1984–1996) were used to draw the total N deposition contours. Nitrogen deposition patterns reveal that the Beartooth Mountains are an area of lower total N deposition than the Colorado Rockies.



rates were determined according to the constant flux : constant sedimentation rate (CF:CSR) model (Oldfield and Appleby 1984). The results are essentially the same as those from the constant rate of supply model, but the CF:CSR model provides a more conservative sedimentation rate. The stratigraphy of ^{210}Pb activity also verifies the stratigraphic integrity of the core.

Distribution patterns in central Rocky Mountain lakes

The distribution of phytoplankton in the Beartooth region was examined by collecting a series of vertical profiles from seven lakes during June and July of 2001 and 2002 (Table 2). Two of these lakes, Island and Beartooth, were repeatedly sampled every 3 days during a 3-week period starting at the end of June in 2002. This approach was included here because this 3-week period encompassed ice-off and the establishment of thermal stratification. Because the majority of wet deposition in alpine regions falls as snow, alpine lakes typically receive the largest influx of nitrate during the spring thaw (Baron and Campbell 1997); thus, nutrient concentrations were rapidly changing over the course of this sampling period. The other five lakes in the data set were stratified when sampled. None of the lakes had low oxygen concentrations in the hypolimnion.

For each profile, samples were collected every 3 m in the water column down to 21 or 24 m with a horizontal van Dorn bottle. The chlorophyll maximum, located between 9 and 12 m in all lakes, was measured using in vivo fluorometry and confirmed by total cell counts. Samples for phytoplankton enumeration were preserved with Lugol's iodine solution. A suite of physical and chemical variables were measured: temperature, pH, conductivity, photosynthetically active radiation, TN, TP, nitrate, soluble reactive P, dissolved Si, and particulate C, N, Si, and P. These particulate data were used to calculate C:N, C:P, N:P, Si:N, and Si:P seston ratios.

Temperature, pH, conductivity, and photosynthetically active radiation were measured with a Hydrolab® multiparameter probe (Hach Environmental, Loveland, Colorado). Dissolved nutrient samples were collected by filtering through prerinsed 0.4-μm polycarbonate filters and analyzed by standard methods (American Public Health Association 2000). Nitrate plus nitrite was measured by the Cd reduction method and soluble reactive P by the ascorbic acid method. Dissolved Si was measured by the heteropoly blue method. Material retained on the polycarbonate filters was analyzed for particulate P by persulfate digestion followed by measurement of soluble reactive P and for particulate Si by sodium carbonate digestion followed by measurement of soluble reactive Si. Particulate C and N were collected on Whatman GF/F filters (Whatman Inc., Clifton, New Jersey) and measured via combustion and gas chromatography with a Carlo Erba 1106 elemental analyzer (Carlo Erba Instruments, Milan, Italy). TP and TN were estimated by summing dissolved and particulate measurements of each nutrient (micromoles per litre). This approach provides conservative low-end estimates of total nutrient pools because dissolved organic fractions are not represented.

Phytoplankton species composition at each depth was determined in duplicate by settling 50-mL aliquots of water in an Utermöhl-style chamber and examining through a Nikon TS-100 inverted phase-contrast microscope (Nikon Inc.) at 400× magnification. Four transects were generally counted

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Fig. 2. Dated (by excess ^{210}Pb activities) sediment profiles of *Asterionella formosa* and *Fragilaria crotonensis* from a set of representative lakes in the (*a*) central (Beartooth–Absaroka Wilderness) and (*b*) southern (Colorado) Rocky Mountains of the United States. Increases in either taxon generally begin after 1950. Diatom relative abundances and ^{210}Pb chronologies were determined by the methods outlined in Saros et al. (2003) and Wolfe et al. (2003).

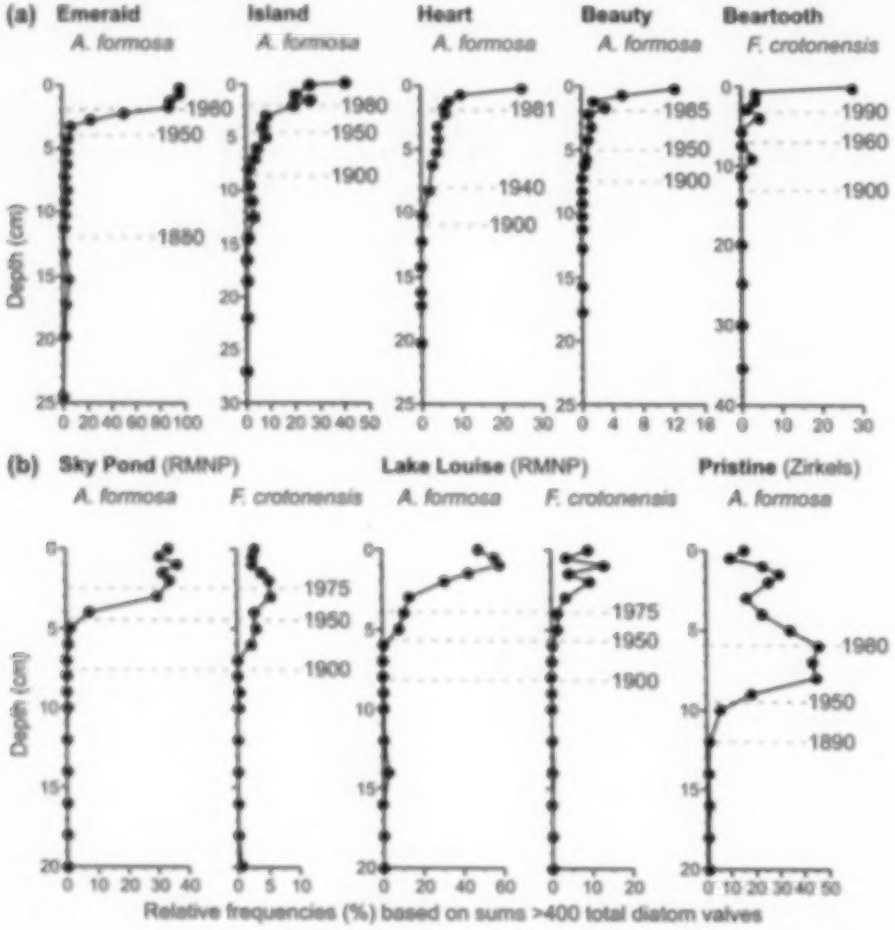

Table 2. Location and select characteristics of the seven lakes used to assess distribution patterns of *Asterionella formosa* and *Fragilaria crotonensis* in the Beartooth Wilderness.

Lake	Location	Elevation (m)	Area (ha)	Z_{max} (m)	Chl max. (m)	1% PAR depth (m)	DOC (mg·L^{-1})	pH	Conductivity (μS·cm^{-1})	Alkalinity (mg·L^{-1})
Beartooth	Park Co., Wyoming	2713	44.5	26.2	12	14.5	1.1	7.6	30.0	19.7
Beauty	Park Co., Wyoming	2874	36.4	35.1	9	22.8	0.8	6.9	7.0	7.2
Fossil	Carbon Co., Montana	3018	66.7	45.7	16	26.1	0.5	6.7	6.0	2.4
Heart	Park Co., Wyoming	3162	16.2	45.7	11	14.0	NA	7.3	6.4	NA
Island	Park Co., Wyoming	2901	59.1	30.5	9	11.0	1.4	7.1	7.0	5.8
Kersey	Park Co., Montana	2460	47.8	20.7	8	8.2	2.1	7.2	20.0	11.0
Long	Park Co., Wyoming	2941	32.4	13.4	9	8.4	1.5	7.0	10.0	7.1

Note: Light profiles were collected in July 2003, and water chemistry data are based on one sample collected from a depth of 2 m in each lake at that time. Z_{max}, maximum depth; Chl max., depth of the chlorophyll maximum when the light profiles were collected; PAR, photosynthetically active radiation; DOC, dissolved organic carbon; NA not available.

for each sample, but additional transects were added when needed to ensure a minimum count of 500 cells per sample. Cell counts for each taxon were converted to the percentage of the total assemblage that each comprised. The distributions of *A. formosa* and *F. crotonensis* were examined separately following Interlandi et al. (1999) using

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Table 3. Initial nutrient conditions in the lake water used in the enrichment experiments.

	Dissolved nutrients			Seston ratios						
Lake	PO_4	NO_3	Si	C:N	C:P	N:P	Si:N	Si:P	Total N	Total P
Beartooth	0.04	1.34	36.0	9.9	197	19.9	0.88	17.5	3.94	0.17
Beauty	<0.015	1.43	29.7	10.8	323	30.0	—	—	4.00	0.09

Note: All nutrient concentrations are reported in µmol and are based on duplicate measurements of the lake water sample.

Table 4. Average seston nutrient ratios (determined on a molar basis) in each of the seven lakes investigated, with standard error given in parentheses.

Lake	C:N	C:P	N:P	Si:N	Si:P
Beartooth (n = 26)	10.4 (0.54)	164.9 (9.4)	17.0 (1.3)	0.79 (0.05)	12.0 (0.59)
Island (n = 25)	9.9 (0.23)	227.0 (36.5)	23.4 (3.9)	0.53 (0.03)	11.3 (1.9)
Kersey (n = 3)	8.1 (0.4)	189.4 (17.7)	24.0 (3.3)	0.34 (0.03)	9.3 (1.8)
Beauty (n = 3)	8.7 (0.8)	227.2 (19.9)	26.3 (2.3)	0.47 (0.02)	12.4 (1.5)
Heart (n = 2)	7.5 (0.05)	46.6 (0.5)	6.25 (0.15)	0.94 (0.06)	5.9 (0.26)
Long (n = 4)	11.0 (1.6)	144.1 (48.5)	11.9 (2.8)	0.32 (0.18)	4.9 (3.0)
Fossil (n = 3)	7.1 (0.74)	168.5 (34.8)	23.7 (2.8)	0.11 (0.02)	2.7 (0.8)

Spearman's rank correlation analysis because most of the data were not normally distributed. To test which variables had the strongest effect on the distribution of each taxon, we explored relationships between the relative abundance of each phytoplankton taxon and the suite of measured physical and chemical variables for the entire data set (n = 66). Because there were 30 correlations attempted per species (15 variables tested in all lakes as well as Beartooth Lake alone), a level of significance of $p \leq 0.002$ (= 0.05/30) was used as a test criterion. The software JMP (SAS Institute Inc., Cary, North Carolina) was used for all correlation analyses.

Response to nutrient enrichment

To augment the observations of natural phytoplankton communities, we conducted two sets of nutrient enrichment experiments. In the first set, lake water was collected from the depth of the chlorophyll maximum (8 m) in Beartooth Lake in July 2002; both *A. formosa* and *F. crotonensis* were among the dominant phytoplankton in this lake at the time (initial nutrient conditions in this water are described in Table 3). Lake water was filtered through a 153-µm mesh to remove large grazers, and four nutrient treatments were created in triplicate: no added nutrients (control), N enrichment (18 µmol N), P enrichment (5 µmol P), and N + P enrichment (18 µmol N + 5 µmol P). Nitrogen was added in the form of $NaNO_3$; P was added in the form of NaH_2PO_4. The amended water was added to 500-mL clear polycarbonate bottles and incubated in the lake for 5 days at a depth of 3 m and a temperature of 14–15 °C. The optical properties of Beartooth Lake are provided in Table 2. At the end of the experiment, triplicate 50-mL subsamples were collected from each bottle and preserved with Lugol's iodine solution for enumeration of phytoplankton, as described above.

In the second set of enrichment experiments, the design and setup were the same except lake water was collected from 9 m in Beauty Lake in July 2003 (Table 3) and five nutrient treatments were created in triplicate based on differing supply ratios: no added nutrients (control), high N:P enrichment (18 µmol N, 1 µmol P), low N:P enrichment (18 µmol N, 5 µmol P), high Si:P enrichment (100 µmol Si, 1 µmol P), and low Si:P enrichment (100 µmol N, 5 µmol P). Silica was added in the form of Na_2SiO_3. The average temperature over the course of the experiment was 11 °C.

Within each set of experiments, a one-way ANOVA was used to identify whether the mean population size for each species differed among treatments. Data were log transformed to meet the assumptions of normality and homogeneity of variance (as assessed with Shapiro–Wilk's test and Levene's test of equality of error variances). When significant differences were found, pairwise comparisons between the control and any of the nutrient treatments were performed using Tukey's honestly significant difference test to protect against inflation of type I errors that can result from making multiple comparisons. The software SPSS (SPSS, Inc., Chicago, Illinois) was used in these analyses.

Results

Distribution patterns in central Rocky Mountain lakes

The main phytoplankton taxa across all lakes in the data set were *A. formosa* and *Dinobryon* sp. Average cell densities across all lakes were 184 cells·mL^{-1} for *A. formosa* and 64 cells·mL^{-1} for *Dinobryon* sp. *Fragilaria crotonensis*, *Tabellaria flocculosa*, and *Aulacoseira alpigena* were also abundant with average cell densities of approximately 10 cells·mL^{-1} for each of these taxa. Cryptomonads such as *Rhodomonas* sp. and dinoflagellates such as *Gymnodinium* sp. were also occasionally present. In general, *Dinobryon* sp. dominated phytoplankton assemblages in the hypolimnia of all lakes, where the chlorophyll maximum occurred, whereas *A. formosa* and *F. crotonensis* were the dominant taxa in the epi- and metalimnia. Average seston nutrient ratios for each lake are provided in Table 4.

The distribution of *A. formosa* across all lakes was positively correlated with C:P, N:P, and Si:P seston ratios (Table 5). For *F. crotonensis*, the strongest correlation was with conductivity, with this diatom comprising a greater percentage of phytoplankton assemblages when the conductivity ex-

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Table 5. Spearman's rank correlation coefficients for the two taxa and environmental parameters that were significant in at least one case, with coefficients reported for the entire data set (All lakes) as well as with data from Beartooth Lake separated out.

	Fragilaria crotonensis		*Asterionella formosa*	
Parameter	All lakes	Beartooth Lake	All lakes	Beartooth Lake
Conductivity	**0.46 (0.0003)**	0.35 (0.10)	0.20 (0.13)	0.31 (0.14)
pH	0.33 (0.01)	**0.70 (0.0001)**	0.37 (0.004)	**0.67 (0.0003)**
C:P	0.078 (0.56)	**0.71 (0.0002)**	**0.44 (0.0005)**	0.44 (0.04)
N:P	0.0059 (0.97)	0.56 (0.008)	**0.43 (0.001)**	0.51 (0.02)
Si:P	0.032 (0.81)	**0.71 (0.0002)**	**0.48 (0.0001)**	0.41 (0.05)

Note: Correlation coefficients in bold were significant ($p \leq 0.002$), with p values given in parentheses. All nutrient ratios are based on micromolar values.

ceeded 10 $\mu S \cdot cm^{-1}$, which only occurred in two lakes in the area. Of the lakes in this data set, the absolute abundance of *F. crotonensis* is by far the greatest in Beartooth Lake, which is situated at the base of a sedimentary butte and has a conductivity that varies around 30 $\mu S \cdot cm^{-1}$. When the distribution of *F. crotonensis* within Beartooth Lake over the 3-week study period is isolated from the rest of the data set, the relationship with conductivity is no longer significant, and positive correlations with C:P, Si:P, and pH are apparent (Table 5); while seston N:P and *F. crotonensis* appeared to be positively correlated, the p value of this association fell just outside the significance level accepted here. In contrast, when the distribution of *A. formosa* is examined in Beartooth Lake alone, the strength of the nutrient correlations remains approximately the same as those in the entire data set.

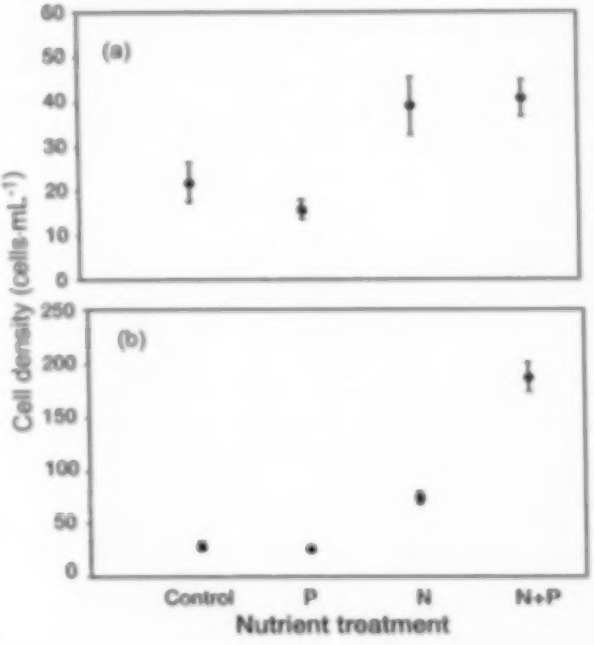
Response to nutrient enrichment

Final cell counts for each treatment in the enrichment experiment in Beartooth Lake are displayed in Fig. 3. For both diatoms, one-way ANOVAs revealed differences among the treatments ($p = 0.001$). Tukey's post hoc comparison between the control and each enrichment treatment revealed that N additions stimulated the growth of *A. formosa* (control:N, $p = 0.039$; control : N + P, $p = 0.015$), whereas P additions had no effect ($p = 0.63$). The number of *F. crotonensis* cells increased approximately threefold with N enrichment ($p = 0.001$), whereas P additions alone had no effect ($p = 0.95$). With the N + P addition, *F. crotonensis* populations were six times greater than in the control ($p < 0.0001$), indicating that this diatom was primarily N limited but upon releasing this limitation also responded to P additions.

In the Beauty Lake enrichment experiment, although *F. crotonensis* was present initially in the samples, the population in each bottle was relatively small (<5 cells·mL^{-1}), yielding high variability in the final cell numbers. This is consistent with the observation about the conductivity tolerance of *F. crotonensis*, as the conductivity in Beauty Lake is 7 $\mu S \cdot cm^{-1}$. Unfortunately, we were unaware of this constraint prior to establishing the experiment. Therefore, the results for this taxon are not reported here.

Differences among the means of the treatments were observed for *A. formosa* ($p < 0.0001$) (Fig. 4). Compared with the control, *A. formosa* populations were greater in the high-N:P treatment ($p < 0.0001$) followed by the low-N:P treatment ($p = 0.039$). However, a comparison of the means between the high- and low-N:P treatments indicated no significant difference ($p = 0.10$), so either combination of N and P enrichment stimulated the growth of this diatom. As mentioned above, the amount of N added in either case was the same; only the concentration of P was altered, with more being added to the low-N:P treatment. Neither treatment involving Si and P enrichment promoted growth above that observed in the control (Fig. 4).

Fig. 3. Results of the nutrient enrichment experiments in Beartooth Lake for (*a*) *Asterionella formosa* and (*b*) *Fragilaria crotonensis* with nutrient treatment indicated for each treatment ($n = 3$). Error bars reflect standard error estimates.



Discussion

The distributions of both *A. formosa* and *F. crotonensis* were associated with the same nutrient parameters, showing positive correlations with C:P and Si:P seston ratios; *A. formosa* was also strongly correlated to seston N:P ratios.

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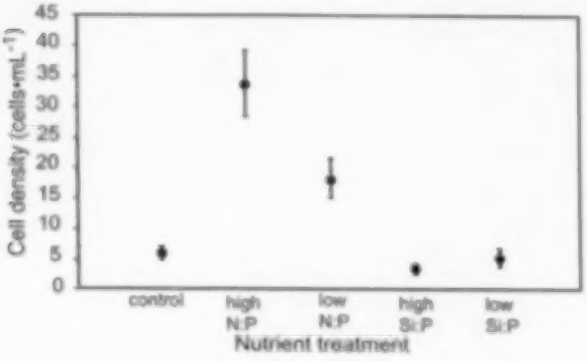
Fig. 4. Results of the nutrient enrichment experiment in Beauty Lake for *Asterionella formosa* with the nutrient supply ratio indicated for each treatment ($n = 3$). Error bars reflect standard error estimates.



These taxa are thus abundant at times when P availability is very low. This further suggests that these diatoms have moderate to high N and Si requirements in these systems, similar to those observed in large lakes of the Greater Yellowstone Ecosystem (Interlandi et al. 1999) and consistent with the results of Michel (2003). The positive correlation between *F. crotonensis* and conductivity may explain why increases in this species are not as widespread in dilute alpine lakes of the western United States as those of *A. formosa*.

In all cases in our experiments, both taxa responded strongly to N enrichment, whereas P enrichment alone had no effect on either species. In addition, although distribution patterns in the Beartooth lakes and previous studies of temperate ecotypes of *A. formosa* indicate a high Si requirement (Tilman 1981), Si enrichment in the Beauty Lake experiment did not stimulate its growth.

The resource requirements of *A. formosa* and *F. crotonensis* populations have been previously investigated at lower elevations in the Greater Yellowstone Ecosystem. Interlandi (2002) estimated N-limited Monod-type growth parameters for both species and found that *A. formosa* had a significantly lower half-saturation constant value than *F. crotonensis*. Roh (2000) evaluated Si and N limitation among these and other species and found both *A. formosa* and *F. crotonensis* to have relatively low N requirements using both internal stores and growth rate data. That study also showed a distinction between these species, indicating that *F. crotonensis* had higher N requirements than *A. formosa*. Together, these studies suggest that *F. crotonensis* may be more dependent than *A. formosa* on increases in N availability in the Beartooth lakes but that it would not take much additional N availability to allow both species to flourish. These two species appear to be good at competing for N compared with some other commonly studied diatom taxa (e.g., *Tabellaria* sp. and *Synedra* sp.), but *A. formosa* is the better of the two.

The role of low-P conditions favoring the growth of *A. formosa* and *F. crotonensis* should not be overlooked, however, as several lines of field evidence point in this direction. As mentioned above, the positive correlations of *A. formosa* and *F. crotonensis* with C:P, N:P, and Si:P ratios found in our study and others in the region (Interlandi et al. 1999) are strong evidence of this connection. Paleolimnological surveys in the Yellowstone area also yielded strong correlations between fossil abundance of *A. formosa* and sediment C:P, N:P, and Si:P ratios, in direct agreement with data from the living communities in these lakes (Interlandi et al. 2003). Whether the mechanism regulating P drawdown in the Beartooth region is greater N availability or something else, like longer growing seasons owing to climate moderation, may remain a bit of a question; however, the evidence for higher N levels is strong.

While the P requirements of both diatoms appear to be low in both alpine and temperate (Tilman 1981) lakes, TP optima determined by modern sediment calibration sets in temperate systems (Fritz et al. 1993; Reavie and Smol 2001; Ramstack et al. 2003) are generally between 13 and 25 $\mu g \cdot L^{-1}$. Hence, both diatoms are abundant in meso- to eutrophic waters. *Asterionella formosa* and *F. crotonensis* are two of several diatom taxa indicative of modest eutrophication by P enrichment in temperate lakes. In the Beartooth lakes, these taxa have increased substantially over the last 30 years, but TP concentrations in these lakes are almost always below 6 $\mu g \cdot L^{-1}$, and neither diatom responded to P enrichment alone in our experiments. This suggests that, owing to the formation of biogeographically distinct ecotypes, caution must be exercised when extrapolating nutrient requirements across a broad spectrum of ecosystems.

Our results confirm that the recent increases in these two diatoms in western alpine lakes of the United States are the result of N enrichment in these systems. Evidence suggests that the source of this increased N loading is atmospheric deposition of anthropogenically fixed N, as rates of N deposition have increased across this region during the last half of the twentieth century (Williams and Tonnessen 2000; Interlandi et al. 2003) and $\delta^{15}N$ values of sedimentary organic matter declined with the shifts in diatom assemblages (Wolfe et al. 2001). Other potential changes in N biogeochemistry may be associated with fish introductions, primarily brook trout (*Salvelinus fontinalis*). However, changes in sedimentary diatom profiles have been observed in lakes both with and without stocked populations (Wolfe et al. 2003). Furthermore, the phytoplankton community shifts recorded in the Beartooth lakes postdate stocking by several decades (Saros et al. 2003). Indeed, McNaught et al. (1999) have suggested that trophic cascading in alpine lakes may be weak or rare owing to the typically high C:P seston ratios in these systems. Coupled with the absence of additional catchment-scale human activities in these wilderness watersheds, we surmise that atmospheric deposition of N is the only viable mechanism to account for the dramatic and widespread reorganizations of phytoplankton communities in western alpine lakes.

In conclusion, the indication that enhanced atmospheric N deposition is driving increases in *A. formosa* and *F. crotonensis* populations is not unexpected in the Colorado Front Range, as this area is in close proximity (<50 km) to agricultural, urban, and industrial centers along the Denver – Boulder – Ft. Collins corridor. Enhanced limnetic dissolved inorganic N concentrations (Caine 1995; Baron et al. 2000) and episodic headwater acidification (Williams et al. 1996) have already been reported on the eastern slope of the Front Range, an area with some of the highest rates of N deposi-

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tion in the western United States (National Atmospheric Deposition Program/National Trans Network 1984–1996). The Mount Zirkel Wilderness Area, 80 km to the northwest, has a significantly lower population density but lies downwind of large coal-fired power generating facilities at Hayden and Craig (Colorado), which are deemed fully capable of augmenting N deposition to ecologically relevant levels. In contrast, lakes in the Beartooth Mountain Range are situated in an area of low N deposition and thus might not be expected to show signs of nutrient enrichment. However, in recent years, the same shifts in diatom communities have occurred here, which is consistent with the observation that alpine lake communities have a low resistance to disturbance and that the threshold at which community reorganizations can occur is quite low. An additional point is that the largest phytoplankton species reorganizations in the Beartooths postdate those observed in Colorado alpine lakes by several decades, which is entirely consistent with the progressive regionalization of ecological impacts associated with anthropogenic N deposition (Vitousek et al. 1997). The widespread diatom community shifts reported here, coupled with robust ecophysiological data supporting their association with enhanced N availability, imply that more profound ecological changes can be expected in alpine wilderness lake of the conterminous United States if N deposition rates continue to increase. The integration of diatom resource ecology and paleolimnology is a powerful new approach towards pinpointing biogeochemical shifts associated with anthropogenic nutrient fluxes.

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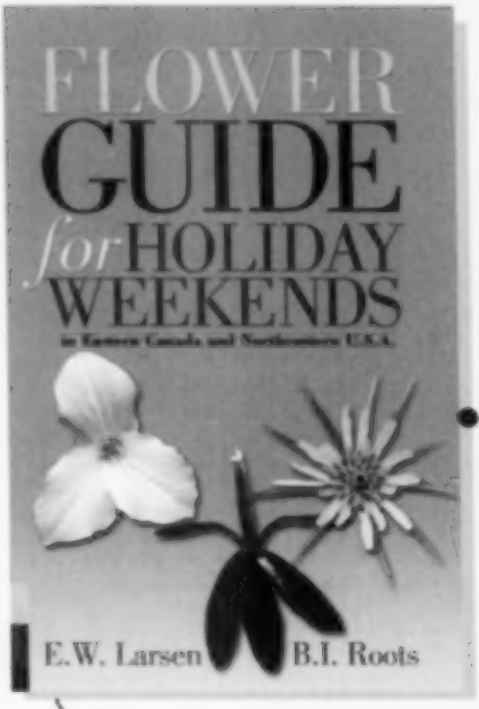

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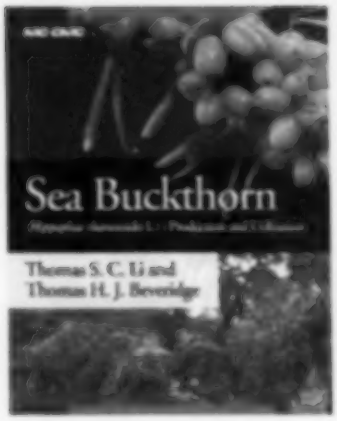

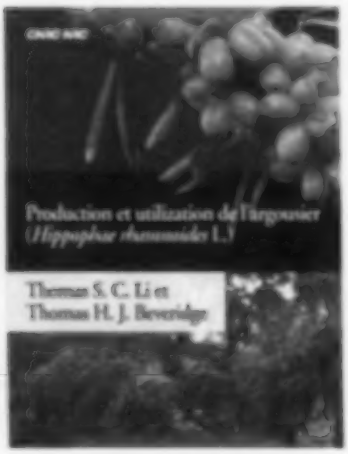

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